University of Alberta

Scaling Leaf Area Index and Rainfall Interception in Lodgepole Pine

by

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Dedication

To my wife Tanja, and sons Andrew, and Matthew

I love you all

Abstract

The objectives of this research were to develop alternate approaches to scale effective leaf area index (LAIe) and rainfall interception storage capacity (S) over time and space using broadly available stand metrics for lodgepole pine in West-Central Alberta. Stand LAIe ranged from 0.03-4.24 (m^2/ m^2) and was very strongly related to total annual stand volume growth across study sites (r^2=0.83, $p<0.001$) suggesting broadly available forest growth data can to used to predict changes in LAIe as stands develop and age. Canopy rainfall interception losses accounted for 23-37% of total growing season rainfall and contrary to expectation, LAIe was a very poor predictor of S. However, because rainfall stored by boles probably played a larger role in interception than leaf area, total stand volume was a strong predictor of S (r^2=0.90, p=0.012). This work also shows that stemflow should not be neglected in interception studies as has been suggested by others.

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Table of Contents

Chapter 1 Introduction 1

Forest Leaf Area 1

Rainfall Interception 3

Research Outline/Objectives 4

References 6

Chapter 2 Leaf Area and Volume Growth Dynamics of Lodgepole Pine 9

Introduction 9

Materials and Methods 11

Site Selection 12

Volume Sampling 12

Volume Growth Estimation 13

Leaf Area Estimation 15

LAIe Estimation Methods 17

Results 19

Stand Characteristics 19

LAIe-Age Relationship 19

Stand Leaf Area 20

Growth Efficiency 21

Discussion 22

Leaf Area 22

Leaf Area and Volume Growth 24

Growth Efficiency 25

Tables and Figures 28

References 45

Chapter 3 Rainfall interception Dynamics of Lodgepole Pine 50
Introduction 50
Materials and Methods 52
Site Selection 52
Interception Measurements 53
Summer 2003 53
Summer 2004 54
Results 57
Stand Characteristics 57
Gross Precipitation and Throughfall 58
Stemflow 58
Rainfall Interception Storage Capacity 59
Discussion 60
Throughfall and Stemflow 60
Interception 63
Scaling Interception to the Landscape Level 63
Conclusions 64
Tables and Figures 65
References 78
Chapter 4 Synthesis 81
Management Implications 84
Future Research 86
References 89
Appendix 3-1 Tipping Bucket Rain gage Calibration 91

List of Figures

Figure 2-1 Map of study area showing all volume growth/LAIe sites. 28

Figure 2-2 a) Height-diameter relationship for young lodgepole pine stands (<5 years), and b) Height-diameter relationship for older lodgepole pine stands (>5years old) 29

Figure 2-3 LAI plot size determination and sun shield configuration for the LAI-2000. 30

Figure 2-4 Typical volume sampling and LAIe plot configuration.ring. 31

Figure 2-5 a) LAIe-age relationship for stands >= 18 S.I., and b) LAIe-age relationship for all stands. 33

Figure 2-6 LAIe-total stand sapwood area relationship 34

Figure 2-7 Relationship between the LAIe-sapwood area ratio and stand age. 35

Figure 2-8 Relationship between the LAIe-sapwood area ratio and stand density 36

Figure 2-9 Non-linear multiple regression model characterizing the relationship between stand-level LAIe and stand sapwood area..... 37

Figure 2-10 a) Relationship between measured LAIe with the LAI-2000 and LAI derived from allometric equations for stands >= 18 S.I., and b) Relationship between measured LAIe with the LAI-2000 and LAI derived from allometric equations for all stands 38

Figure 2-11 Residual plot of LAIe with respect to site index (observed with the LAI-2000 – predicted LAI using allometric equations)..... 39

Figure 2-12 a) PAI-age relationship for stands >= 18 S.I., and b) PAI-age relationship for all stands. 40

Figure 2-13 LAIe-PAI relationship for stands >= 18 S.I., and all stands. 41

Figure 2-14 Growth efficiency - stand age (years) relationship.. 42

Figure 2-15 Stand density - average live crown length relationship 43

Figure 2-16 a) Growth efficiency - average live crown length relationship for stands <30 years old, and b) Growth efficiency - average live crown length relationship for stands >=30 years old. 44

Figure 3-1 Map of study area, including rainfall interception stands. 65

Figure 3-2 a) Photograph showing a throughfall trough and tipping bucket for BR 1, and b) photograph showing the distribution of throughfall troughs for ER 1. 66

Figure 3-3 a) Photograph showing a stemflow collar and spacers for a PC 1 tree, and b) stemflow collar and collection hose for a tree at PC 1 shortly after a rainfall event. 67

Figure 3-4 Rainfall event size distribution for all five stands. 70

Figure 3-5 a) Stemflow volume-rainfall event size relationship for the PC 1 sample trees, and b) stemflow volume-rainfall event size relationship for the ER 1 sample trees 71

Figure 3-6 Predicted stemflow response to increasing event sizes for all five stands 73

Figure 3-7 Rainfall interception as a percent of gross precipitation for all five stands. 75

Figure 3-8 Rainfall interception - event size relationship for all five stands 76

Figure 3-9 Rainfall interception storage capacity (S) - total stand volume relationship for all five stands 77

List of Tables

Table 2-1 LAIe – volume growth stand descriptions..... 32

Table 3-1 Stand characteristics for the five rainfall interception stands..... 68

Table 3-2 Precipitation and throughfall values for the five stands during the summer of 2003 and 2004..... 69

Table 3-3 Stemflow sample tree characteristics for PC 1 and ER 1..... 72

Table 3-4 a) Summary of predicted stemflow for all five stands, and b) summary of interception and predicted storage capacities for all five stands..... 74

List of Equations

Equation 2-1 $y = \alpha + (1 - \alpha)\gamma^{X}$ 14

Equation 2-2 Estimated past height = measured current height – (predicted current height – predicted past height)..... 15

Equation 2-3 Total volume growth (5-yr) = current gross volume–past (5-yr) gross volume . 15

Equation 2-4 Maximum Distance = Tree Height / Tan 32 17

Equation 2-5 $A_1 = \alpha (A_s)^{\beta} (D)^{\gamma} * 1.24\text{-}5$ 18

Equation 2-6 $Y = x / (\alpha + \beta(x) + \gamma (\sqrt{(x)})$..... 19

Equation 3-1 I = Pg- (TF + SF)..... 53

Equation 3-2 $y = \alpha - \beta\gamma^{x}$ 57

Equation 3-3 Slope = -84.06(ht) + 56.95(dia) + 640.06..... 59

Equation 3-4 Threshold event size (mm) = 0.419(ht) - 0.195(dia) +1.31..... 59

Chapter 1
Introduction

Intensive land use practices coupled with a rapidly growing population has resulted in increasing pressures on Canada's water resources. This issue is extremely important in Alberta, because of the cumulative effects of intensive agricultural operations and disturbances due to oil and gas exploration, forest harvesting, and forest fires, all in the face of a warming, drying climate. The Government of Alberta has also recognized that water resource issues have become increasingly important to all Albertans. Although water has been withdrawn from Alberta's rivers, lakes and aquifers for over 100 years, a fluctuating and unpredictable water supply in recent years has emphasized the need to make some major changes in how to use and allocate this renewable, but finite, resource. As a result, the Alberta government has recently developed a provincial water strategy, "water for life: Alberta's strategy for sustainability" which commits to the wise management of Alberta's water quantity and quality for the benefit of Albertans now and in the future (Alberta Environment, 2003). However, from the beginning of the discussions and consultation for the water strategy, information and knowledge regarding the water resources of Alberta was clearly identified as the most critical element in our ability to manage water effectively (Alberta Environment, 2003).

Because of rapid industrial development in Alberta in the recent decade (particularly in forested regions) one particular area where knowledge is currently weak relates to understanding how a range of land-uses affect the quantity and quality of water. Because the vast majority of water in Alberta is produced from the forested landbase, there is a particular need to understand how vegetation dynamics and man's manipulation of vegetation affects the long-term quality and quantity of water resources produced from this region. This information is needed so that water and watershed values can be protected in long-term landscape level plans.

Forest Leaf Area

The leaf area of forests is the principle forest attribute driving growth, productivity, and forest succession processes (Smith and Long, 2001; Long and Smith, 1992; Dean and Long 1986; Waring 1983, Whitehead et al., 1984; Kira 1975). The leaf area of forest vegetation is also the principle biological feature of forests that interacts with climate to control the water balance of forests by regulating interception and transpiration losses. As a result, many distributed

hydrologic models (Bevan, 1977; Band et al, 1993) rely on estimates of leaf area to predict the hydrologic behavior of forested landscapes, because spatial and temporal variation in leaf area regulates how climate, disturbance, and successional processes affect the hydrology of forested landscapes over time and space.

Because of the high cost involved in direct measurements of leaf area index (LAI) using destructive sampling, forest LAI is most often estimated using indirect approaches including remote sensing (Hall et al., 2003a; Kushida et al., 2004; Chen et al., 2002), allometric relationships with forest stand attributes (Long and Smith, 1988; Dean and Long, 1986), and ground-based optical techniques (Hall et al., 2003b; Leblanc and Chen, 2001; Chen, 1996). Leaf area index can be estimated using remote sensing with satellites though estimates usually need to be ground-truthed using either direct or other indirect sampling approaches. However, because of the pixel spatial resolution of the imagery, independent verification of leaf area using destructive sampling is often impractical or impossible (Hall et al., 2003b). Other techniques such as allometric approaches typically utilize the relationship between tree sapwood area and tree leaf area for a given species based on the "pipe model" theory (Waring et al., 1982). However, over the past several decades, eco-physiological research has shown that most allometric approaches are highly species-specific and can vary depending on differences in site quality, stand density, early stand growth rates and crown class (Whitehead, 1978; Albrektson, 1984; Pearson et al., 1984; Dean and Long, 1986; Espinosa Bancalari et al., 1987; Long and Smith, 1988). Lastly, ground-based optical techniques such as hemispherical photography and instruments such as the LAI-2000 (Li-Cor., 1991) estimate LAI based on measurements of radiation penetration through the canopy. Although these techniques have been developed as an alternative to allometric approaches and can provide fast and more consistent estimates of LAI over larger spatial scales (Wells and Norman, 1991; Fassnacht et al., 1994; Chen, 1996; Cutini et al., 1998), they are limited by assumptions concerning spatial orientation of foliage (shoot and canopy clumping) and requirements for specific lighting conditions (Chen et al., 1997). All of these approaches involve considerable costs or sampling effort which limits their broad suitability for predicting LAI over broad spatial and temporal scales. As a result, there is a need to develop a simpler approach to estimate LAI and enable the scaling of this important forest attribute over time and space.

Because leaf area is the principle attribute driving forest productivity, information on forest growth should contain sufficient information to explain spatial and temporal variation in forest LAI. Previous studies attempting to derive relationships between stand-level tree growth

and LAI have met with limited success because of the confounding effects of different crown classes (Kollenberg and O'Hara, 1999) and differences in growth rates due to variable site productivity and stand structures (Dean et al., 1988; Smith and Long, 1989; Long and Smith, 1990). However, because differences in stand structure among sites affect stand-level productivity (Oliver and Larson, 1996), the inclusion of these factors in the development of stand LAI relationships is likely to improve relationships between forest productivity and LAI. This approach would also allow for broad scaling of LAI as it utilizes broadly available information on stand growth contained in forest inventories. This will also provide insights into how forest productivity and stand level growth efficiency changes as stands develop and mature.

Rainfall Interception

The leaf area of forest vegetation affects water balance in forested landscapes through two main mechanisms, transpiration during photosynthesis, and interception of precipitation. Rainfall interception is the fraction of gross precipitation that is captured by vegetative and soil surfaces and subsequently re-evaporated to the atmosphere. In forests, rainfall interception can account for 10-50% of total annual precipitation (Klassen et al. 1998). As a result, the combination of interception and transpiration losses by vegetation largely regulates runoff dynamics and the production of water from forested landscapes. However, surprisingly little information exists on how interception losses vary among stands of differing species composition, age, and stand condition to enable broad insights into how this important component of stand water balance varies across forest types and developmental sequences.

Research on rainfall interception in forests has historically focused on 2 main categories; 1) simple empirical description of interception in a rather narrow range of stands or stand conditions and 2) process-based interception modeling most often focused on description of water accumulation and subsequent evaporation dynamics from foliage. Although research in the first category has provided insight into magnitude of water losses due to rainfall interception for specific forest species and stand conditions (McMinn 1960; Mahendrappa and Kingston 1982; Frechette 1969; Plamondon et. al. 1984; Valente *et* al. 1997), none of these previous studies utilized independent variables describing interception that would enable scaling interception to other stands, or forest types. Differences in crown form among tree species, height, density, diameter range, crown closure and LAI between different forest types preclude using results from these previous studies to scale interception losses among different forest types. Thus a general

understanding of how interception varies among forests of differing species composition, age, and stand condition remains lacking in the literature. Although more recent process-based interception research (category 2) include estimates of canopy storage (S) (i.e. the maximum amount of moisture that can be held by a forest canopy) in their interception models (Davie and Durocher 1997; Calder, 1986; Gash, 1979; Rutter et al. 1971), S is usually derived from an estimate of canopy closure or cover density for specific stand structures and species compositions. Therefore, these approaches also do not allow for broad prediction or scaling of interception losses since S is typically expressed in terms of canopy closure or cover density for specific stand conditions. In addition, these physically-based models often assume canopy conditions remain constant over time, thereby limiting their applicability at different spatial and temporal scales. In both categories of research, an important issue limiting generalization of results has been use of independent variables that were not robust with respect to species composition, age, and stand condition to describe rainfall interception.

Canopy leaf area is an important stand attribute because it influences interception and transpiration losses, as well as driving growth, productivity, and forest succession processes. Recent interception models (van Dijk and Bruijnzeel, 2001; Hedstrom and Pomeroy 1998) have begun to utilize the relationship between S and LAI in an attempt to account for differences in vegetation type over time and space. However, the broad applicability of such models or use of LAI as a scalar for interception in forest vegetation remains uncertain. Because differences in leaf shape, texture as well as branch and twig inclination among tree species will influence rainfall interception processes, the relationship between LAI and S is likely species specific.

Research Outline/Objectives

The broad objectives of this research were to explore relationships between stand level forest growth and LAI in order to develop an alternative approach to estimating forest LAI using broadly available forest inventory information. A related objective was to explore the sensitivity of rainfall interception dynamics to variation in LAI for lodgepole pine in west-central Alberta.

Chapter 2 of this dissertation describes research focusing on the characterization of LAIe over a range of stand ages and explores the relationship between stand level growth (periodic annual increment or PAI) and LAI in lodgepole pine to determine if available forest growth and yield information could be used as a reliable predictor of changes in forest LAI over broad spatial and temporal scales. A related objective in that study was to explore temporal trends in LAI to

provide insight into how forest water balance is likely to change over the developmental sequence of forest stands. Lastly, in Chapter 2 I explored whether changes in growth efficiency as stands develop and mature could provide additional insights into potential mechanisms involved in declining stand level forest productivity as stands age.

Chapter 3 of this thesis focuses on the characterization of rainfall interception in these same lodgepole pine stands to determine whether rainfall interception processes measured at the tree or stand level can be adequately described using fundamental canopy or stand attributes in order to provide the basic tools required to scale interception processes to the landscape level. The specific study objectives were to determine if stand LAI is a sensitive predictor of differences in rainfall interception losses along a gradient of stand ages/developmental sequences in lodgepole pine. A related objective was to determine if other commonly measured stand metrics typically included in forest stand inventories could be used to scale rainfall interception either alone or in combination with LAI.

In Chapter 4, I summarize results from these two studies to highlight contributions of this work to the literature, discuss broader inferences that can be drawn from the work, and comment on directions for future work.

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Chapter 2

Leaf Area and Volume Growth Dynamics of Lodgepole Pine

Introduction

The leaf area of forests is the principle forest attribute driving growth, productivity, and forest succession processes (Smith and Long, 2001; Long and Smith, 1992; Dean and Long 1986; Waring 1983, Whitehead et al., 1984; Kira 1975). Leaf area of forest canopies govern stand growth by regulating the capture and allocation of light energy through photosynthesis into various components (i.e. above or below ground) of tree growth (Kimmins, 1996), and relationships between forest leaf area, canopy condition, and stand growth dynamics has been the subject of considerable research effort over the past several decades (Waring and Running, 1998). The leaf area of forest vegetation is also the principle biological feature of forests that interacts with climate to control the water balance of forests by regulating precipitation, interception and transpiration losses. Distributed hydrologic models such as TOPMODEL (Bevan, 1977), RHESSys (Band et al, 1993) and many others rely on estimates of leaf area to predict hydrologic behavior of forested landscapes. Thus, leaf area serves as an important link between forests and forest water balance because spatial and temporal variation in leaf area regulates how climate, disturbance, and successional processes affect the hydrology of forested landscapes over time and space.

In order understand and predict these hydro-ecolological relationships, estimates of leaf area among various forest tree species, stand types, as well as their temporal dynamics are essential. However, the direct measurement (destructive sampling) of stand leaf area is costly and extremely time consuming. As a result, stand leaf area is generally estimated using indirect approaches, including remote sensing (Kushida et al., 2004; Hall et al., 2003a; Chen et al., 2002), allometrics (Long and Smith, 1988; Dean and Long, 1986), and ground based optical techniques (Hall et al., 2003b; Leblanc and Chen, 2001; Chen, 1996). However, many of these approaches are limited in their suitability for predicting broad landscape level changes in forest leaf area over space and time.

Estimates of leaf area index (LAI) using satellite remote sensing usually need to be ground-truthed using either direct or other indirect approaches because of both limitations in pixel spatial resolution of satellite thematic mapper (TM) imagery and limitations in the

sensitivity of reflectance values to provide information on LAI. In addition, independent verification of leaf area using destructive sampling is often impractical or impossible due to the pixel spatial resolution of remotely sensed data and therefore is often based on sub-sampling within individual pixels (Hall et al., 2003b). Alternatives to direct sampling using allometric approaches typically utilize the relationship between tree sapwood area and tree leaf area for a given species based the "pipe model" theory (Waring et al., 1982). However, eco-physiological research over the past several decades has shown that species-specific leaf area-sapwood area ratios vary based on differences in site quality, stand density, early stand growth rates and crown class (Whitehead, 1978; Albrektson, 1984; Pearson et al., 1984; Dean and Long, 1986; Espinosa Bancalari et al., 1987; Long and Smith, 1988). Therefore, the use of a constant leaf area-sapwood area ratio to scale LAI over broad spatial or temporal scales will lead to considerable estimation error. Furthermore, attempts to derive local stand-level allometric relationships have met with limited success because they mask tree-to-tree variation that occurs within a stand (Dean and Long, 1986) which can lead to substantial scaling error. As a result, Long and Smith (1988), and Dean and Long (1986) developed allometric relationships for lodgepole pine that attempted to account for this variability by relating individual tree LAI to sapwood area and the height to the midpoint of the live crown. Although their scaling approach improved stand scale estimates of LAI, the ability to scale LAI from the tree to larger spatial scales is difficult and time consuming. Lastly, ground-based optical techniques such as hemispherical photography and the LAI-2000 (Li-Cor., 1991) estimate LAI based on measurements of radiation penetration through the canopy, and have been developed as an alternative to allometric approaches because they can provide faster and more consistent estimates of LAI over larger spatial scales (Wells and Norman, 1991; Fassnacht et al., 1994; Chen, 1996; Cutini et al., 1998). Although these techniques provide an alternative to using allometric approaches to estimate LAI, ground-based optical approaches are limited by spatial orientation of foliage (shoot and canopy clumping) and requirements for specific lighting conditions (Chen, 1997a).

All of the forgoing approaches require considerable cost or sampling efforts that limit their suitability for predicting forest LAI over broad spatial and temporal scales. As a result, there is a need to develop simple techniques to accurately estimate LAI based on either limited sampling requirements or using existing data. Since forest leaf area is the principle attribute driving forest productivity, broadly available information on stand level tree growth should contain sufficient information to explain variation in stand LAI over time or among stands. However, previous attempts to derive relationships between stand level tree growth and LAI have

met with limited success because of difficulties in scaling from tree to stand scales related to the confounding effects of crown class (Kollenberg and O'Hara, 1999) and differences in growth with variable site productivity and stand structure (Dean et al., 1988; Smith and Long, 1989; Long and Smith, 1990). As these stand attributes are well established sources of variation in stand level productivity (Oliver and Larson, 1996), including these factors in the development of stand LAI relationships is likely to substantially improve relationships between forest productivity and LAI as well as providing additional insight into how forest productivity and stand level growth efficiency changes as stands develop and mature.

The objectives of this study were to explore the relationship between stand level growth (periodic annual increment or PAI) and LAI across a broad range of stand ages in lodgepole pine to determine if available forest growth and yield information could be used as a reliable predictor of changes in forest LAI over broad spatial and temporal scales. A related objective was to explore temporal trends in LAI to provide insight into how forest water balance is likely to change over the developmental sequence of forest stands. Lastly, to examine if changes in growth efficiency as stands develop and mature could provide additional insight into potential mechanisms involved in declining stand level forest productivity as forests age.

Materials and Methods

This research was conducted in even-aged managed and unmanaged stands of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) throughout the west-central portion of Alberta, Canada in Natural Sub regions 10 (Upper Foothills) and 11 (Lower Foothills) (Archibald et al., 1996; Beckingham et al., 1996) . All stands within each sub region were located on "d" and "e" ecosites. In general, stands were located in the region between Sundre and Swan Hills, and Drayton Valley and Hinton (Fig 2-1). Stands were located within 4 Forest Management Agreement Areas (FMA's) including Sunpine Forest Products Ltd., Weyerhaeuser Ltd, Sundance Forest Industries Ltd., and Weldwood Ltd. The region ranges in elevation from 920m to 1280 m. Mean temperatures for January and July are approximately –12°C and 15°C respectively. Average annual precipitation for the region range from 540 to 640mm, with approximately 370mm to 450mm falling as rain (Environment Canada, 2002)

Site Selection

A broad range of stands varying in age and canopy leaf areas were sampled. Only fully stocked (full site occupancy), pure (90% or greater) lodgepole pine growing on good sites (>16 site index (SI) at reference age 50yrs; Huang et al. (1997)) were selected for measurement. Other minor species present in the stands included trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera*) in sub region 10 and 11, and balsam fir (*Abies balsamifera*) in sub region 10. Potential stands were identified using age class distribution maps for lodgepole pine provided by the various forest companies as well as digital maps (GIS) containing site quality information. In addition, potential stands could not contain visual indicators of insect or disease attacks that might affect volume growth or leaf area.

A reconnaissance was carried out on potential stands identified on maps to determine stand age, species composition, stocking, forest health, and site index. Stand age was estimated from increment cores from 3-4 randomly located trees within the stand. Cores were taken at stump height (30 cm) and angled down toward the point of germination. Only cores reaching the pith were used to determine stand age. Preliminary site index was estimated using procedures similar to those outlined by Huang et al. (1997). In each stand, three randomly located, large diameter trees were cored at breast height (1.3m) to determine age. Tree heights were determined using a Vertex Hypsometer III (Haglöf Sweden AB.). The Vertex was calibrated twice daily (1 morning 1 at noon) to account for variation in air temperatures during the day. An approximate site index was then determined using the DBH, age, and height based on sub region specific SI tables provided by Huang et al. (1997). Site index for stands less than three years old at DBH was estimated from an adjacent mature stand of lodgepole pine using the same procedures outlined above. Stands not meeting this initial selection criteria (fully stocked, pure pine, SI>16 m) were not selected for sampling. However, in some instances, preliminary site index estimates indicated that the stand was suitable (>16m S.I), but when a plot was established, the actual site index was less than 16. These border line stands were included because it was difficult to find stands covering a full age range with a site index >16. A total of 29 stands were measured. Seventeen stands were naturally regenerated (presumably fire-origin), and 12 were artificially regenerated using drag scarification (none of the stands were planted).

Volume Sampling

Twenty-eight stands were sampled for volume growth, nine in sub region 10 and nineteen in sub region 11. One very young stand (1 year old) was not sampled for volume and volume

growth because a 5-year volume growth increment calculation was not possible. Once suitable stands had been identified, a location representative of average stand conditions was located and a plot center established. Although some stands contained a mixture of species, volume growth plots were established within regions in the stand that were dominated by 100% lodgepole pine. Plot centers were located at least 2 tree heights away from any stand boundary (road, cut edge, pipeline etc.) in order to avoid edge effects. One circular fixed radius plot was established in each stand. Plot radii varied among stands depending on stand density; plot sizes were designed to sample approximately 30 trees/plot. Plot sizes ranged from $5m^2$ (90,000 trees per hectare (tph)) to $500m^2$ (400 tph). Within each plot, the total tree height and height to base of live crown of each tree was measured with the Vertex Hypsometer. Stem diameters were measured at 2 different heights depending on stand age. The diameters of "younger trees" (less than 5 years old at breast height (1.3m)) were measured at 30cm above the ground and "older trees" (greater than 5 yrs old at breast height) were measured at 1.3 m. Although 1.3m is typically the default for the measurement of tree diameters (i.e. diameter at breast height (DBH)), it was necessary measure the diameter of "younger trees" at some height less than breast height in order to get an estimate of 5-year diameter and volume growth. With trees less than 5 years-old at breast height this was not possible. The height of 30cm above the ground was chosen because it is another standard point of measurement (i.e. stump height) in the forest industry.

Increment cores or cookies were sampled from each tree depending on tree size. In general, cookies were sampled from trees < 3cm at (1.3m), and all trees where diameter was measured at 30 cm. For the larger trees, 2 increment cores were taken per tree with a 5 mm increment corer; one on the north side and one on the south side. The sapwood radius was recorded for every core and cookie in the field immediately after they were extracted by holding the sample up to the sunlight and observing and marking the transition between translucent sapwood to opaque heartwood. All increment cores with intact bark were stored in plastic straws for increment measurement in the lab. Cookies were placed in re-sealable bags. All samples were stored in a cooler during field sampling and frozen each night for final storage.

Volume Growth Estimation

Five-year diameter growth was measured for all core and cookie samples to the nearest 0.1 mm using a stage micrometer in the lab. Cookies were prepared for analysis by shaving one surface with a razor blade in order to see the rings more clearly. Radial increment was determined for each core (2 per tree) and for opposite sides of each cookie (2 measurements/cookie).

Measurements were taken from the inside bark diameter and counted towards the pith 5 years (5 rings), including the current years ring. Diameter growth was determined by multiplying the average radial growth from the two samples per tree by 2. For trees 5 yrs old at 1.3m or 30cm, radial growth was determined by measuring from the inside of bark to the center of the pith. Bark thickness was measured to the nearest 0.1mm with a stage micrometer on every core and cookie (each side) for a total of 2 measurements per tree. Average bark thickness per tree was determined by taking an average of the two measurements.

Sapwood areas were calculated by measuring the average sapwood radius per tree similar to the procedure used for determining diameter increment. Sapwood width (to the nearest 0.1 mm) was determined using a stage micrometer for each core (2 per tree) or for opposite sides of each cookie (2 measurements/cookie) from inside bark to the sapwood-heartwood boundary previously delineated in the field. An average sapwood width was then determined by averaging the two measurements. Individual tree sapwood area was estimated by subtracting the heartwood area ((average total tree radius - average sapwood radius)^2 * pi) from the total cross sectional area or basal area of the tree (inside bark) assuming the cross section of the tree was circular.

In order to estimate periodic volume growth, an estimate of individual tree height 5 years before sampling was required. Past heights were estimated using two height-diameter relationships derived from all trees sampled in the study. One relationship was derived for trees whose diameters were measured at DBH, and the other for trees measured at 30cm. The general form of the equation was (Equation 2-1):

Equation 2-1 $y = \alpha + (I - \alpha)\gamma^X$

Where: y is the predicted height, X is the tree diameter, α is the asymptote corresponding to $X \rightarrow \infty$, I is the intercept of the y–axis (the value of y when X=0), and γ describes the rate at which y changes from its initial value I to its final value at ∞ (Ratkowsky, 1990). A least-squares non-linear regression procedure was used to estimate parameters in equation 1. The parameter I was treated as a fixed parameter to more closely reflect the attributes being estimated by equation 1. For example, in the older stands I=1.3m, this corresponds to the height of the tree when its diameter is 0cm at DBH (1.3m) (although the height could theoretically be less than 1.3m it could be no more than 1.3m). Similarly, a value of I=0.3m was chosen for the younger stands where the diameters were measured at 30cm. All stands with trees less than 5 years old at 1.3m were considered young stands (n=3) and stands with all trees greater than 5 years at 1.3m were

considered older stands (n=25). All trees from all stands in each of these two groups were combined in the determination of tree height-diameter relationships (Figure 2-2a and 2-2b). Using these relationships the height 5 years before sampling could be estimated based on past diameter (calculated by subtracting the average 5-year diameter growth for each tree from current diameter (outside bark)). However, because the predicted current height for some trees (based on current diameter) varied from the measured current height, a correction for estimated past height was applied as follows (Equation 2-2):

Equation 2-2 Estimated Past height = Measured Current Height – (Predicted Current Height – Predicted Past height)

Equation 2-2 employs the difference between predicted current and predicted past heights as a scalar to apply a correction to the measured current height in order to estimate past height. Current and past volumes were calculated for every tree sampled in this study, and volume growth was determined by (Equation 2-3):

Equation 2-3 Total volume growth (5-yr) = Current gross volume – Past (5-yr) gross volume

Individual tree volumes were calculated using Equation 2-3, based on measured current heights and diameters for current tree volumes, and estimated past height obtained from Equation 2-2 and measured past diameters for past volume. Individual tree volumes were calculated using two approaches (1) sub-region specific individual tree gross volume equations developed by Huang (1994) for lodgepole pine, and (2) using the formula for a cone (i.e. 1/3 basal area x height). It was necessary to use method 2 because Huang's (1994) taper equations use the diameter at breast height (DBH) as an input in the model and not all trees in the study were 1.3m tall. As a result, the volume growth of three stands (those defined as "younger stands" earlier) was estimated using the second approach.

Leaf Area Estimation

Limitations of Optical Techniques for Estimating LAI

An optical approach using the LAI-2000 (Li-Cor, 1991) for estimating LAI was adopted in this study. Optical techniques estimate LAI indirectly by correlating leaf area with the probability of light penetration through the canopy using a gap fraction formula defined by Miller

(1967). The LAI-2000 is a portable light sensor system designed to measure diffuse light, using five concentric light-detecting silicon rings that receive radiation from five sky sectors centered on zenithal angles 7°, 23°, 38°, 53°, and 68°. The LAI-2000 also contains an optical filter to restrict detected radiation to wavelengths below 490nm. Using two LAI-2000 units, above (A) and below canopy (B) measurements are taken simultaneously and the ratio of measured A:B radiation in each ring reflects the canopy gap fraction for each detector. Estimates of LAI by the LAI-2000 are based on the following four assumptions (Li-Cor, 1991):

1. The foliage is black (only sky radiation is seen by the sensor beneath the canopy, since radiation striking foliage is absorbed)
2. The foliage is randomly distributed in the canopy,
3. The foliage elements are small (less than four times the distance of the closest foliage element to the sensor), and
4. The foliage is azimuthally randomly oriented.

Although real canopies rarely, if ever strictly meet all of these assumptions, several procedures can be used to minimize their effects on estimating LAI. To meet the first assumption, measurements should be taken under uniform overcast skies or at dawn or dusk in order to minimize the effect of direct beam radiation. The LAI-2000 underestimates true LAI when measurements are taken under sunlit conditions because of illumination of foliage elements (causing leaves to appear brighter than the sky) and due to an increase in blue light scattering by foliage (Leblanc and Chen, 2001; Chen et al. 1997a; Wells and Norman 1991). In addition, the LAI-2000 cannot distinguish between photosynthetically active and inactive tissue. As a result, LAI estimates using the LAI-2000 will include leaves, stems, and branches and is synonymous with a "plant area index" (L_a) defined by Chen et al. (1997b) Furthermore, the LAI-2000 will tend to underestimate true LAI when foliage elements are clumped (assumption 2), as is the case in many coniferous forests (Chen and Chilar, 1995). Needles are clumped together in shoots, shoots are clumped on branches and branches are clumped into distinct crowns. Nilson (1971) defined Ω, (often referred to as the clumping index) as a parameter determined by the spatial distribution pattern of leaves. When the foliage is randomly oriented, Ω is unity, when the foliage elements are regularly distributed, Ω is less than unity, and when the foliage elements are clumped, Ω is greater than unity. Effective LAI can be thought of as product of the clumping index and the plant area index (Chen et al. 1997b). For these reasons, it has been suggested that the LAI-2000 measures "effective" LAI (LAIe) rather than true LAI (Leblanc & Chen 2001; Chen et al. 1997a, Chen et al. 1997b).

Although procedures have been developed to address the clumping issue (Chen and Chilar, 1995; Stenberg et al., 1994), they are labor intensive, costly and very time consuming. As a result, I, like many others (Nackaerts, et al., 2000; Le Dantec et al., 2000; Strachan and McCaughey, 1996; Dufrêne and Bréda, 1995), chose to use LAIe as an indicator of stand leaf area.

LAIe Estimation Methods

Average stand LAIe, corresponding to the volume sampling plots was estimated for 29 stands (including the 1-yr old stand) using the LAI-2000. Two LAI-2000 units were used; one located in an adjacent opening to automatically record above (outside) canopy (A) readings at 15 second intervals and one used to manually measure below canopy (B) readings. In order to minimize the effect of direct foliage illumination and blue light scattering, LAIe sampling was targeted for overcast days or at dawn or dusk, however, in some instances, sampling under less than ideal conditions was unavoidable. In all situations, the open sensor was fitted with a cardboard shield to block any direct sunlight from hitting the sensor (Figure 2-3). In addition, below canopy measurements were made with the sensor in the shade avoiding taking measurements within sunflecks. LAIe was calculated based on detector rings 1-4 (Stenberg et al. 1994) using the C2000 software provided with the LAI-2000 (Li-Cor, 1991).

To ensure leaf area estimates were representative of the volume sampling plots, below canopy LAIe measurements were taken from the perimeter of a fixed radius plot whose plot center was the same as the volume-sampling plot (Figure 2-4). However, the size of the LAIe plot varied (was scaled) between stands based on the average stand height. Because the lower limit of view from ring 4 in the LAI-2000 is 58° from zenith (32° from horizontal) the maximum distance between the sensor and a tree that would still include that tree in the LAIe estimate is given by Equation 2-4:

Equation 2-4 $$\text{Maximum Distance} = \frac{Tree\ height}{Tan\,32}$$

Equation 2-4 was used to scale the LAIe sampling plot radius to include only the trees sampled in the volume growth plots in the LAIe estimate. The trigonometric relationship between maximum distance and tree height is also reflected by a constant of 1.6 multiplied by tree height.

Prior to sampling, the average stand height was determined on 3 trees using a vertex. The plot diameter was then determined to be 1.6 times the average stand height (Figure 2-3).

Both above canopy and below canopy sensors were equipped with either 90° or 45° view restrictors in order to remove the operator from the field-of-view, and to restrict sampling to within the plot. The 90° restrictor was typically used; however, in some stands it was difficult to find openings large enough for the open (above canopy) sensor due to obstructions. In all cases, both sensors were equipped with the same view restrictor. LAIe measurements were then taken at points along the plot perimeter facing in, towards the plot center. When the 90° restrictor was used, 8 sampling points located at N, E, S, W, NE, SE, SW, and NW along the boundary were used. When the 45° viewcap was used, additional points at NNE, ENE, ESE, SSE, SSW, WSW, WNW, and NNW were also sampled for a total of 16 sampling points. All below canopy measurements were made at 50cm above the ground surface.

LAI was also estimated using allometric relationships for lodgepole pine developed by Long & Smith (1988) and Dean & Long (1986) for mature trees and saplings, respectively. Both relationships utilize relationships between LAI, sapwood area and distance to the midpoint of the live crown. The general form of the equation is given by Equation 2-5:

Equation 2-5 $A_l = \alpha (A_s)^{\beta} (D)^{\gamma} * 1.24$

Where A_l is the tree leaf area in m^2, A_s is the sapwood area in cm^2 (measured at 1.3m for the mature trees and at 25cm for the saplings), D is the distance from measurement height of the sapwood area (1.3m or 25cm) to the center of live crown in meters, and 1.24 is the correction factor for the area of fresh needles to account for needle shrinkage after drying. I used the coefficients for mature trees reported by Long & Smith (1988) (α=0.064, β=1.43, and γ=-0.73) and for saplings reported by Dean & Long (1986) (α=0.021, β=1.47, and γ=-0.14) for determining allometric estimates of LAI for these stands. The allometric equation for mature trees was applied to all stands where the diameters and sapwood area were measured at 1.3m (i.e. the "older" stands (n=25) and the equation for sapling trees was applied to stands where the sapwood area was measured at 30cm (i.e. the "younger" stands n=3). In order to determine the plot or stand level LAI based on Equation 2-5, A_l (m^2) from every tree in the plot was summed and divided by the total plot area (Kollenberg and O'Hara, 1999; Smith and Long, 1989)

Results

Stand Characteristics

Stands ranged in age from 1 to 133 years and were mostly fire-origin however some younger stands were artificially regenerated using drag scarification (Table 2-1). In all cases, stand density in managed young stands was broadly similar to stocking after fire, and high enough to be considered full site occupancy. Stand densities ranged from 400-90000 tph (trees per hectare), and co-varied (negatively) with stand age. Though the objective was to sample "good" site quality stands (SI>16 m), site indices ranged from 13.2m to 22.7m (at reference age 50yrs), with an average SI for all stands of 19.1m (S.E. 0.438) including, three stands with site indices less than 16m. Average stand height ranged from 0.05m to 25.5m at 1 and 133 years respectively, and average stand volumes ranged from 7.15m^3/ha at age 6 to 560.83m^3/ha at age 100.

The mean stand basal area for all 28 stands was 34.33 m^2/ha (s.d. 10.45 m^2/ha), and ranged from 14.19m^2/ ha at age 6 to 52.72m^2/ha at age 27 (Table 2-1). However, basal area remained fairly constant at about 40m^2/ha from age 36 years onward. Basal area in stands 17 years of age and less was composed almost entirely of sapwood. The transformation of sapwood to heartwood began to appear in trees roughly in stands between 17 to 19 years of age. The development of stand sapwood area with age mirrored that of average stand basal area. Maximum stand sapwood area of 44.52m^2/ha also occurred at approximately 27 years. It is also interesting to note that unlike the relatively constant average stand basal area from 36 to 133 years, the average stand sapwood area generally declined during this same time period.

LAIe-Age Relationship

Measured LAIe values ranged from 0.03 at age 1 to a maximum of 4.24 in stand O99 at age 20. Across the 29 stands, LAIe increased rapidly in younger age classes reaching a peak at around 25 yrs of age followed by a gradual decline as stands continued to age (Table 2-1). The relationship between LAIe and stand age for "good sites" (>= 18m S.I.) is shown graphically in Figure 2-5a, and was described using the Gunary (Ratkowsky, 1990), three-parameter nonlinear regression model (Equation 2-6):

Equation 2-6 $Y = x / (\alpha + \beta(x) + \gamma(\sqrt{(x)})$

Considering only stands with SI>=18m (equal to or above the median SI for "good" sites), this function described the variation in LAIe with age well. The resulting parameters where α = 19.0054, β = 1.0396, and γ = -7.4411 (r^2 = 0.777, $p<0.0001$, n=22). When all stands (including those from "medium" sites) were included in the model, there was still a significant relationship between stand age and LAIe, but was more variable (r^2=0.594,$p<0.0001$) (Figure 2-5b). The predicted maximum LAIe was 3.21 when only the good sites were included, and 3.11 when all stands were considered. Although maximum LAIe values differed slightly in magnitude, the model indicated maximum LAIe's for both occurred at 25 years of age. It is interesting to note that the general form of the relationship in both cases are very similar and exhibit several similarities. It is not surprising that the shapes of the curves are similar since they are derived using the same model, however both curves predict maxima at 25 years.

Stand Leaf Area

LAIe-Sapwood Area Relationship

Though LAIe generally increased with total stand sapwood area, the relationship was not linear (Figure 2-6). LAIe increased rapidly to a plateau with average stand sapwood area. The lack of a linear relationship between LAIe and SA was associated with high variability in LAIe-SA ratios among stands. However, the variability in LAIe-SA ratios were not well correlated to any single stand attribute. For instance, changes in LAIe-SA ratios were poorly explained by changes in stand age showing strong variability within stands of the same age and between stands of different ages (Figure 2-7). Similarly, only a weak statistical relationship with density was observed (Figure 2-8). However, when individual stand attributes generally related to leaf area development dynamics were combined in a stepwise multiple regression, density(D), age(A), sapwood area(S), and the changes in sapwood area with age (interaction of age and sapwood area (A*S)) explained most of the variation in LAIe across the 29 stands (Figures 2-9a and 2-9b).

Allometric LAI

Measured LAIe from all sites was then plotted against allometric estimates of LAI. Individual tree sapwood areas for some trees in 4 of the 28 stands could not be measured accurately due to broken and crumbled cores. As a result, the allometric estimation of LAI was carried out for the remaining 24 stands. Estimated LAI using allometric relationships showed linear (near 1:1) relationships with LAIe measured with the LAI-2000. The relationships for stands with SI>=18 (Figure 2-10a) were stronger (r^2=0.7696, $p<0.0001$, n=18) than when all

stands regardless of SI were included (r^2 = 0.6567, p<0.0001, n=24) (Figure 2-10b). An examination of the residuals from this relationship indicates that the allometric equation of Long and Smith (1988) under-estimates LAI in stands with lower productivity or SI (Figure 2-11). Although the relationship is weak, the allometric equations under-predicted estimated LAIe for 5 of the 6 stands with site indices less than 18m, however as site index increased, this bias seemed to disappear.

Leaf area and stand volume growth

Five-year periodic annual increment (PAI) for the 28 stands ranged from 1.42m^3/ha/yr at 6 years to 13.79m^3/ha/yr at 20 years (Table 2-1). Consistent with relationships evident for LAIe, PAI increased rapidly in juvenile stands reaching a peak between 20-30 years followed by gradual decline as stands aged beyond this. The same non-linear model form as used for LAIe-age relationship provided a very good fit to this relationship. Considering only stands with SI>=18m (Figure 2-12a), this function described the variation in PAI with age well (r^2 = 0.558, p<0.0001, n=21). When all stands (including those from "medium" sites) were included in the model, the relationship between stand age and LAIe was more variable (r^2 = 0.526, p =<0.0001, n=28) (Figure 2-12b). Both models predict a maximum PAI at 25 years, with PAI of 10.3m^3/ha/year and 9.9m^3/ha/yr for stands greater than 18m S.I., and all stands, respectively. It is also interesting to note that maximum PAI occurs at approximately the same age where both maximum BA/ha and SA/ha was also reached.

The general similarity in relationships between LAIe-age and PAI-age were reflected in a strong linear relationship between LAIe and PAI (Figure 2-13). For stands with SI>=18m the linear relationship was very strong (r^2 = 0.8307, p<0.0001). When all stands (including those from "medium" sites) were included in the model, the relationship became somewhat weaker (r^2 = 0.6796, p<0.0001)

Growth Efficiency

Consistent with the general form of the relationships for LAIe and PAI, relationships of growth efficiency (GE) ((m3/ha/yr)/LAIe) with age closely paralleled the relationships of LAIe and PAI with increasing stand age (Figure 2-14). The same non-linear function used for LAIe and PAI was used to describe this relationship as well (r^2=0.31, p<0.0001). Maximum average GE of stands was 3.15 m^3/m^2 and occurred between 23 and 27 years, coinciding in time with the peaks of both LAIe and PAI. Interestingly, there was no significant relationship between GE and site

index for the stands in this study (r^2=0.002, p=0.94). Similarly, there was no relationship between stem density and GE (r^2=0.058, p=0.22).

However, GE was related to stand characteristics related to leaf area and crown attributes. A strongly negative log-linear relationship (r^2=0.945) between stand density and live crown length was evident across the stands sampled in this study (Figure 2-15). Though the relationship between GE and average live crown length for all stands in this study was not strong, when stands in developmental phases up to and including the approximate time of crown closure (30 yr) were considered separately from post-canopy closure stands (>30 yr), GE was related to differences in average live crown length. Prior to canopy closure, GE increased with increasing crown depth (Figure 2-16a), although the relationship was weak (r^2=0.34, p=0.06). However, for stands after canopy closure (Figure 2-16b), GE showed a strong decline in stands with increasing crown length (r^2=0.24, p=0.04) suggesting that stand level GE is related to the organization and distribution of foliage within the canopy.

Discussion

Results from this study clearly illustrate that canopy leaf area increases rapidly in the early phases of stand development in lodgepole pine reaching a peak fairly early in the stand's developmental sequence followed by a slower and steady decline as stands continue to age. The description or prediction of this change in LAIe in lodgepole pine as forests age has important implications for both understanding how forest water use might change as stands establish, grow, and mature, and in providing additional insight into how forest productivity changes as stands age.

Leaf Area

This pattern of development in LAIe with stand age I observed in Lodgepole pine is consistent with the relationships others have found for lodgepole pine (Long and Smith, 1992) and other early successional species (Gholz, 1986; Kira and Shidei, 1967). However the rate of change in LAIe including rate of initial development, timing of peak LAIe, and subsequent changes in maturing stands will vary depending on individual stand characteristics such as initial stocking density, the rate of self-thinning, and site quality (Long and Smith, 1992; Turner and Long, 1975; Assmann, 1970). For instance, Long and Smith (1992) found that lodgepole pine reached peak LAI between 40-45 years in the Medicine Bow Mountains of south-central Wyoming, while I found that peak LAIe occurred between 20 and 30 years in west-central

Alberta. While differences in climatic regimes (total precipitation, snowfall, growing season temperatures, etc.) between Wyoming and Alberta are likely partially related to differences in timing of peak LAI between this study and that of Long and Smith (1992), differences in stand productivity are probably the most likely reason for differences between the two studies. I focused my sampling on highly productive stands (SI>16 m) whereas Long and Smith (1992) sampled stands from a broad range of site qualities and densities. The mean productivity class of stands I sampled (SI = 19.1m (SE=0.44)) was significantly higher ($p<0.005$) than those (SI=17.6m (SE=0.25m)) sampled by Long and Smith (1992). Because of the relationship of LAI with both stand productivity and stand dynamics such as self-thinning (Reid et al., 2003), subtle differences in the initial development of LAI, timing of peak LAI, and subsequent decline in LAI in maturing stands between these two studies is likely due to differences in stand productivity. Although it is not well known why the peak stand level LAI is followed by a steady decline in older maturing stands, several hypotheses including increasing crown shyness, decreases in stem water transport capacity, shifts is carbon allocation patterns, and decreases in photosynthetic efficiency in older stands have been suggested (Ryan et al., 2004; Ryan and Yoder 1997, Long and Smith, 1992; Smith and Long, 2001).

General relationships between the maximum leaf area a tree can support and the ability of stems to transport water to tree crowns (sapwood area and sapwood hydraulic conductivity) are well established (Whitehead et al. 1984, many others) and numerous studies (Kaufmann and Troendle, 1981; Kaufmann et al., 1982; Pearson et al., 1984; Dean and Long, 1986) have used leaf area sapwood area ratios (LA:SA) as the basis for allometric approaches to estimate stand or landscape level LAI. However, despite more recent research confirming variation in LA:SA ratios with tree age (Ryan and Yoder, 1997), crown class (Reid et al., 2003, Thompson, 1989), stand density (Keane and Weetman, 1987), and stand productivity (Coyea and Margolis, 1992; Long and Smith, 1988) researchers continue to use this approach (Medhurst and Beadle, 2002; Mencuccini and Bonosi, 2001; Turner et al., 2000; Medhurst et al., 1999; Penner and Deblonde, 1996; Pothier and Margolis, 1991). Although variation in LA:SA ratios with age has been previously reported for individual trees, the present study is the first (to my knowledge) to show a clear change in stand level LA:SA ratios in maturing stands. My results provide additional rationale for questioning the usefulness of this approach to scaling leaf area in forests. Furthermore, given observations of declining sapwood hydraulic conductivity with age, the additional decrease in LA:SA ratios observed in this study strongly support the assertion by Ryan

and Yoder (1997) that decline in stand productivity in maturing stands is, at least in part, driven by changes in sapwood hydraulics and crown water relations.

Aside from approaches based solely on LA:SA, other approaches to scaling stand leaf area based on additional stand attributes may work reasonably well. In my study, the LAI predicted from allometric equations (Long and Smith, 1988; Dean and Long, 1986) agreed favorably with measured LAIe despite differences in climate between Alberta and Wyoming & Utah (respectively). This provided an independent confirmation that the measured LAIe using optical techniques (LAI-2000) in my study were reasonable. Although Long and Smith (1988) argued that their equation was robust across stands with variable productivity (unbiased with respect to SI), I found that by restricting my analysis to stands constituting a narrower range of SI ("good" sites only) the relationship of measured LAIe to LAI predicted using allometric relationships improved, thus suggesting a descriptor of site productivity might improve the allometric approach.

Leaf Area and Volume Growth

The results from this study show that there is a very close relationship between volume growth (m^3/ha/yr) and age. I observed both strong linear relationships in LAIe with PAI and very similar trends between LAIe & age and PAI & age. This finding is consistent with relationships previously reported for lodgepole pine by Long and Smith (1992). Volume growth (PAI) in my study peaked at 9.9 m^3/ha/year at 25 years (when all stands ere considered) coinciding in time with the peak in LAIe. Long and Smith (1992) found that peak volume growth (10m^3/ha/yr) also coincided with peak LAI for their stands but occurred later, between 40-45 years of age. This has implications for prediction of LAI for both hydrological and ecological research over broad spatial and temporal scales. Given the broad availability of forest growth and yield information in most forested regions of North America, the use of PAI as a predictor of LAIe provides a useful and relatively easy approach to the description of spatial and temporal variability in LAIe across larger landscapes. While actual LAI at peak LAIe is probably species specific, once peak LAIe is determined for individual species, the approach of using PAI to describe temporal trends as stands develop and age provides a powerful tool to scale LAIe to across space and time (stands of differing age and prediction of how these are likely to change over longer time scales).

While the basis for pursuit of these relationships are based on the broad recognition that because leaves are the primary sites of photosynthesis driving tree growth, there should be a relationship between stand level growth and stand level leaf area, previous research has not been

particularly successful in establishing this relationship. Kollenberg and O'Hara (1999) found only a weak positive relationship (r^2=0.34) between average volume growth (m^3/ha/yr) and LAI for multi-aged lodgepole pine stands in Montana. Although PAI-LAI relationships for even-aged lodgepole pine stands have generally been stronger than those of multi-aged stands (Dean et al., 1988; Smith and Long, 1989; Long and Smith, 1990), the relationships previously described between volume growth and LAI at the stand scale have been somewhat weak. Smith and Long (1989) suggest that the productivity of forest stands is strongly influenced by stand structure. Differences in crown morphology affect carbon allocations among stems, branches, and foliage (Ford, 1985). However, characterizing these differences is complicated because differences in age and site quality affect stand structure and productivity (Assmann, 1970). In contrast to the variable results obtained by Kollenberg and O'Hara (1999), Dean et al. (1988), Smith and Long (1989), and Long and Smith (1990), the generally good relationships I observed were likely due to the fact that I restricted my sampling to stands within the same productivity class and thus did not include the strong confounding influence of these other stand attributes related to stand structure. This also suggests that differences in stand productivity or site index should be included in derivation of broader process based stand productivity relationships.

It is also important to note that most studies dealing with stand productivity/leaf area relationships estimate LAI using allometric techniques based on a combination of sapwood area-leaf area relationships measured at the individual tree level and scaled to the stand level. The procedure I used to estimate LAI is an indirect technique based on light attenuation through the canopy and is essentially an indirect measure of stand structure, since LAIe measured by the LAI-2000 is proportional to the logarithm of the gap fraction. The amount, distribution and spatial orientation of foliage within individual crowns and throughout the entire canopy determines light capture by the canopy (Pinno et al., 2001; Kellomaki et al., 1995). Therefore light capture by the LAI 2000 implicitly measures stand structure and thus provides a plausible explanation for the strength of the relationships I found.

Growth Efficiency

The changes in growth efficiency I observed across the range of stand ages considered in this study, provide additional insight into factors involved in both leaf area and productivity as stands age. The relationships I observed between LAIe, PAI, and GE with stand age were all generally similar with maximum GE, LAIe and PAI, all occurring at approximately 25 years. Although, reasons for the post-peak decline in LAI and PAI are not well understood, Smith and Resh, (1999), Smith and Long (1989), and Assmann (1970), suggest that a reduction in GE

shortly after canopy closure (maximum LAI) is one of the more likely reasons for declining volume growth in latter stages of stand maturation. However, the specific mechanisms governing these changes in GE are presently unclear.

Paradoxically, consistent with findings of Long and Smith (1992) for lodgepole pine and Waring (1983) for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), I observed no relationship between GE and LAIe, PAI, or other stand characteristics such as SI or stand density despite strong similarity in the pattern of GE, LAIe, and PAI with stand age. When I compared stands of widely differing densities, many of the higher density stands were found to have higher GE despite lower LAIe and this may be related to differences in crown and foliar attributes among stands of differing stem density. I observed a strong negative exponential relationship between average live crown length and stem density, thus higher density stands with greater GE were stands with short live crowns suggesting trees with compact crowns concentrating foliage near the top of the tree where light exposure is presumably greatest are the more efficient at producing stemwood. Indeed, live crown lengths were generally shorter in higher density stands with greater GE. This notion is supported by similar assertions by Smith and Long (1989), and Tadaki, (1986) who suggest leaf efficiency (synonymous with GE) is highest for canopies with foliage concentrated near the top of the canopy (i.e. trees with short compact crowns).

These results imply that as crown closure occurs and light resources become limited below the canopy, trees maintain those foliage elements that are most efficient at driving photosynthesis in order to maximize net primary productivity. Prior to canopy closure, leaf area accumulates as a direct consequence of lengthening crowns and production increases with increasing leaf area, (i.e. the negative effect of lengthening crowns is offset by the increase in leaf area). After canopy closure, when maximum leaf area is attained, decreasing GE associated with lengthening crowns results in declining stemwood production (Smith and Long, 1989). After a stand has achieved canopy closure, trees direct more resources towards stemwood production rather than the development of and maintenance of branches, foliage, and roots which impose additional respiratory demands. In fact, 70% of the total canopy mass of young lodgepole pine forests is composed of foliage and branches, compared to 30% for older forests composed of larger trees (Smith and Long, 2001; Smith and Long, 1989).

There was no direct relationship between density and GE for the stands in this study, however, the relationships between density and crown length and between crown length and GE were strong (especially for stands > 30 years old). Although density and its influence on live crown length seem to provide a plausible explanation for the decline in GE, others have suggested

that the production: respiration ratio or changes in canopy water relations could be responsible as well (Ryan et al., 2004; Ryan and Yoder, 1997; Mitchell and Goudie, 1980). As it is highly unlikely that one single set of factors govern changes in stand productivity with age, combinations of several factors are probably involved. My results support suggestions by both Smith and Long (1989) that differences in canopy architecture and stand structure in even-aged stands of lodgepole pine directly influence stand volume growth and growth efficiency, and those of Ryan and Yoder (1997) that changes in crown water supply are implicated in declining growth as stands age.

Tables and Figures

Figure 2-1 Map of study area showing all volume growth/LAIe sites.

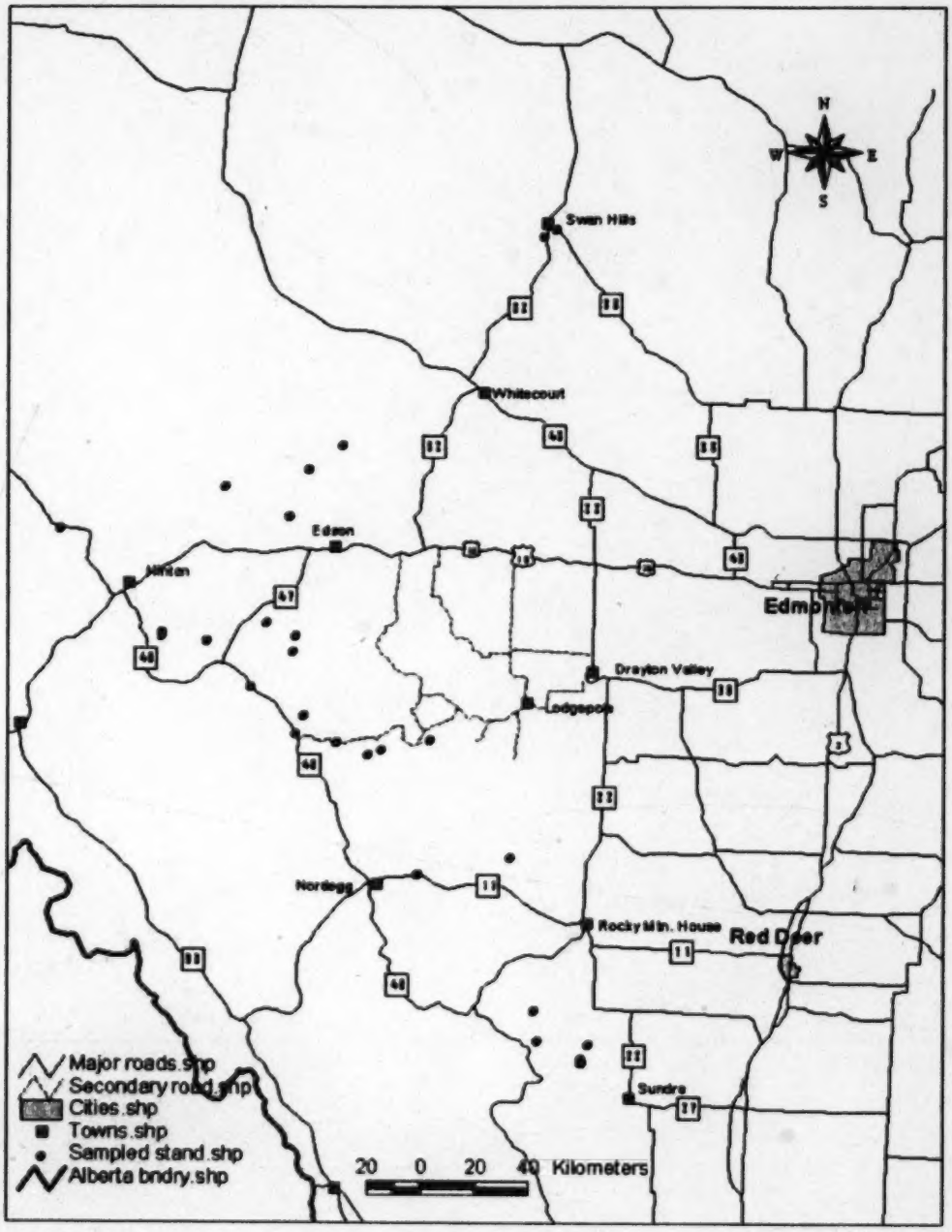
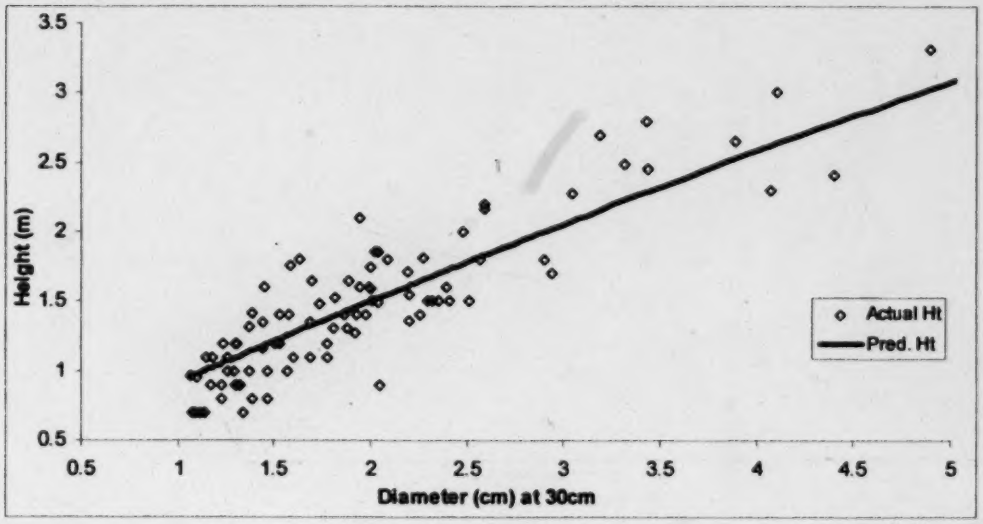


Figure 2-2a) (Top) Height-diameter relationship for young lodgepole pine stands (<5yrs old at DBH (1.3m)). The predicted height based on Equation 2-1: (y) $= \alpha + (I - \alpha)\gamma^x$, Where: α=12.12718, γ=0.947829, x=diameter (cm), and I= 1.3) n=93, and b) (Bottom) Height-diameter relationship for older lodgepole pine stands (>5 years old at DBH (1.3m)). The predicted height (y) $= \alpha + (I - \alpha)\gamma^x$, Where: α=36.24455, γ=0.963104, x=diameter (cm), and I= 1.3) n=798.



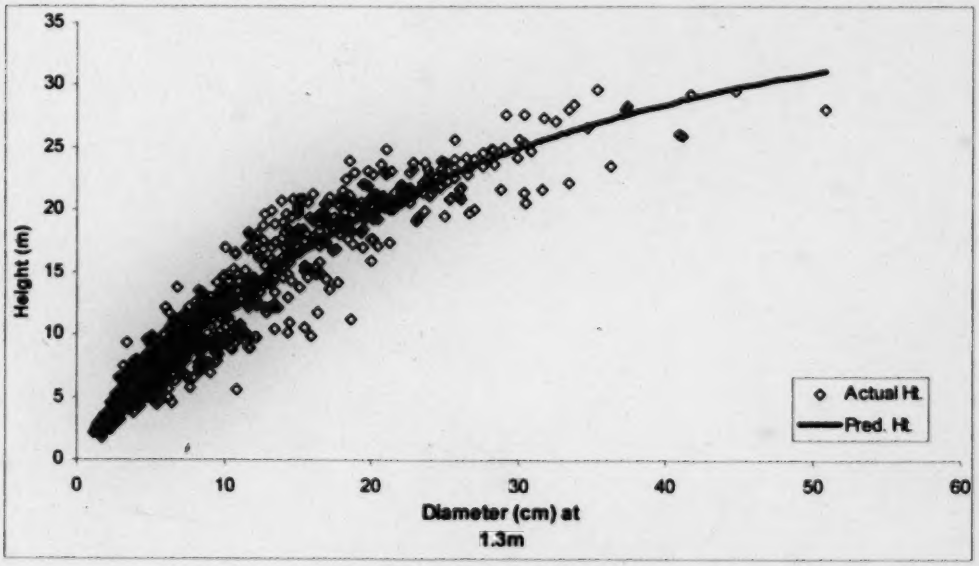


Figure 2-3 LAI plot size determination and sun shield configuration for the LAI-2000.

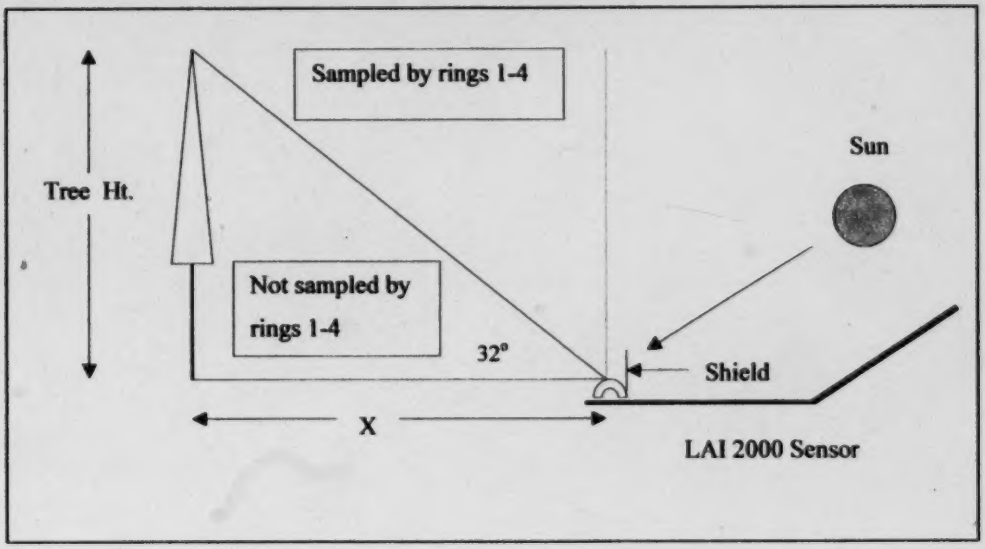


Figure 2-4 Typical volume sampling and LAIe plot configuration. Dashed lines indicate the lower limit of the LAI-2000's fourth ring. The solid vertical lines indicate the extent of the LAIe sampling plot. Dark trees sampled by the LAI-2000, light trees not sampled.

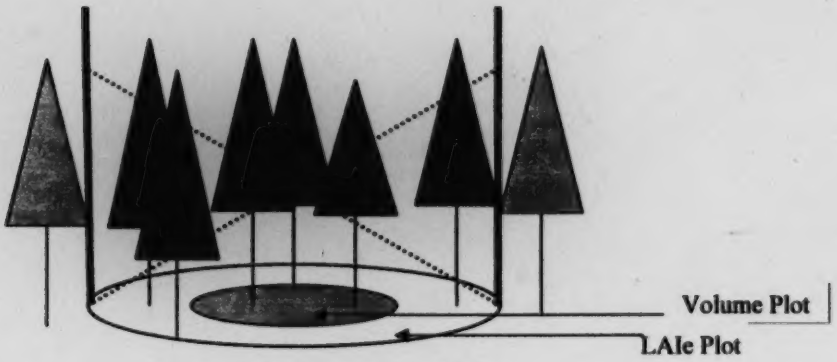


Table 2-1 LAIe and volume growth stand

Stand Name[a]	Latitude (Deg, Min)	Longitude (Deg, Min)	Subregion[b]	Stand Age	Site Index	Density (tph)	Average Stand Height (m)	Total Volume (m^3/ha)	PAI (m^3/ha/yr)	Basal Area (m^2/ha)	Sapwood Area (m^2/ha)	LAIe m^2/m^2
O 89[d]	53 05.4911	-116 33.1230	11	1	20.5	11000	0.05	-	-	-	-	0.03
CA 6[d]	52 00.0156	-114 59.0012	11	6	20.1	90000	1.16	7.15	1.42	14.19	14.19	0.92
Elk 105[d]	52 56.4070	-116 24.6740	11	10	20.4	41000	1.81	12.34	2.12	14.85	14.85	0.85
BS 6[d]	51 55.3476	-114 54.0312	11	14	20.5	36000	3.07	26.41	4.28	19.76	19.76	2.70
BS 12[d]	51 54.6948	-114 54.0756	11	17	20.8	24000	4.98	111.22	13.22	29.65	29.65	3.19
Swan 22[f]	54 40.0788	-115 23.0568	10	19	17.3	30000	4.51	78.77	8.71	26.03	25.47	2.96
OS9[d]	53 00.3810	-116 32.2884	11	20	20.6	20000	6.45	170.14	13.79	40.20	35.63	4.24
Rig 21[d]	51 58.6020	-115 08.6790	11	21	18.1	14000	4.69	77.09	8.58	20.91	20.39	2.92
Lynx 23[d]	53 45.2322	-117 05.0754	10	23	21.9	11200	6.90	101.21	7.27	23.99	20.98	2.62
SD Robb 24[d]	53 13.2702	-116 37.6458	11	25	21.6	10333	8.47	161.86	6.55	28.25	24.24	2.46
Al 23[f]	52 04.6722	-115 10.1616	11	27	22.7	10000	11.23	344.86	13.41	52.72	44.52	3.60
Swan 32[f]	54 41.8278	-115 19.1724	10	28	17.1	29000	7.54	184.47	10.20	41.76	36.81	4.13
OWL-15[d]	52 54.8454	-116 05.7798	11	30	22.1	3600	9.22	134.51	10.19	24.94	21.42	3.23
SC1[f]	52 34.8636	-115 21.1812	11	35	16.6	8000	8.06	119.82	5.14	23.14	19.08	2.15
PC-1[d]	52 56.7918	-116 35.0028	10	36	18.0	7000	9.14	199.87	6.79	39.42	29.07	2.60
SD 17[d]	53 16.2876	-116 37.2882	11	40	22.1	5500	13.24	329.28	9.45	40.42	28.93	2.83
S120[f]	53 55.4646	-116 26.5842	11	42	19.7	6800	10.42	249.73	7.32	36.43	28.68	2.73
J37[f]	53 14.1066	-117 21.9660	10	44	19.1	5200	13.03	311.13	9.35	43.41	32.74	2.86
BS 40[f]	51 58.4202	-114 52.0068	11	47	18.1	5800	11.60	269.90	8.76	38.04	18.53	2.76
Gregg 34[f]	53 14.8668	-117 21.8838	10	48	13.2	12400	7.78	150.68	6.69	28.47	15.91	1.39
BR-1[f]	52 57.5256	-115 50.1030	11	51	18.1	2800	15.79	400.59	9.77	44.83	27.58	2.95
Edson 60[f]	53 40.3494	-116 42.4170	11	55	20.4	1500	17.95	328.64	7.19	32.98	20.31	2.41
Tower 66[f]	52 30.2424	-115 51.0510	10	72	18.7	1550	19.93	497.84	6.56	47.93	27.71	2.69
Tower 1[f]	53 13.8516	-117 06.5712	10	90	17.8	1550	18.92	456.53	4.73	44.33	20.71	2.72
RL 100[f]	53 33.6930	-117 59.3010	10	100	18.8	1350	22.23	560.83	5.67	41.09	18.56	2.16
ER-1[f]	52 55.6500	-116 21.1206	11	113	18.3	1250	20.59	495.25	4.34	44.66	17.95	1.75
OWL-6[f]	52 53.7564	-116 10.0890	11	115	13.9	3100	17.16	443.20	5.63	45.82	28.58	2.64
MI 1[f]	53 18.5814	-116 47.5788	11	130	15.6	1500	20.61	423.02	5.45	38.09	16.34	2.93
BS 120[f]	51 54.6516	-114 53.7378	11	133	20.7	400	25.46	441.85	3.98	34.81	16.01	1.78

[a] Stand Name. [d] refers to drag scarified stands, and [f] refers to fire-origin stands

[b] Subregion 10 refers to Upper Foothills Natural Sub-Region, 11 refers to Lower Foothills Natural Sub-Region

Figure 2-5a) (Top) LAIe / Age relationship for stands >= 18 S.I. ($y = x / (\alpha + \beta(x) + \gamma(\sqrt{(x)})$), Where $\alpha = 19.0054$, $\beta = 1.0396$, and $\gamma = -7.4411$ ($r2 = 0.777$, $p<0.0001$ n=22) and b) (Bottom) LAIe / Age relationship for all stands ($y = x / (\alpha + \beta(x) + \gamma(\sqrt{(x)}))$, Where $\alpha = 14.6527$, $\beta = 0.8789$, and $\gamma = -5.7192$ ($r2 = 0.593$, $p<0.0001$, n=29)

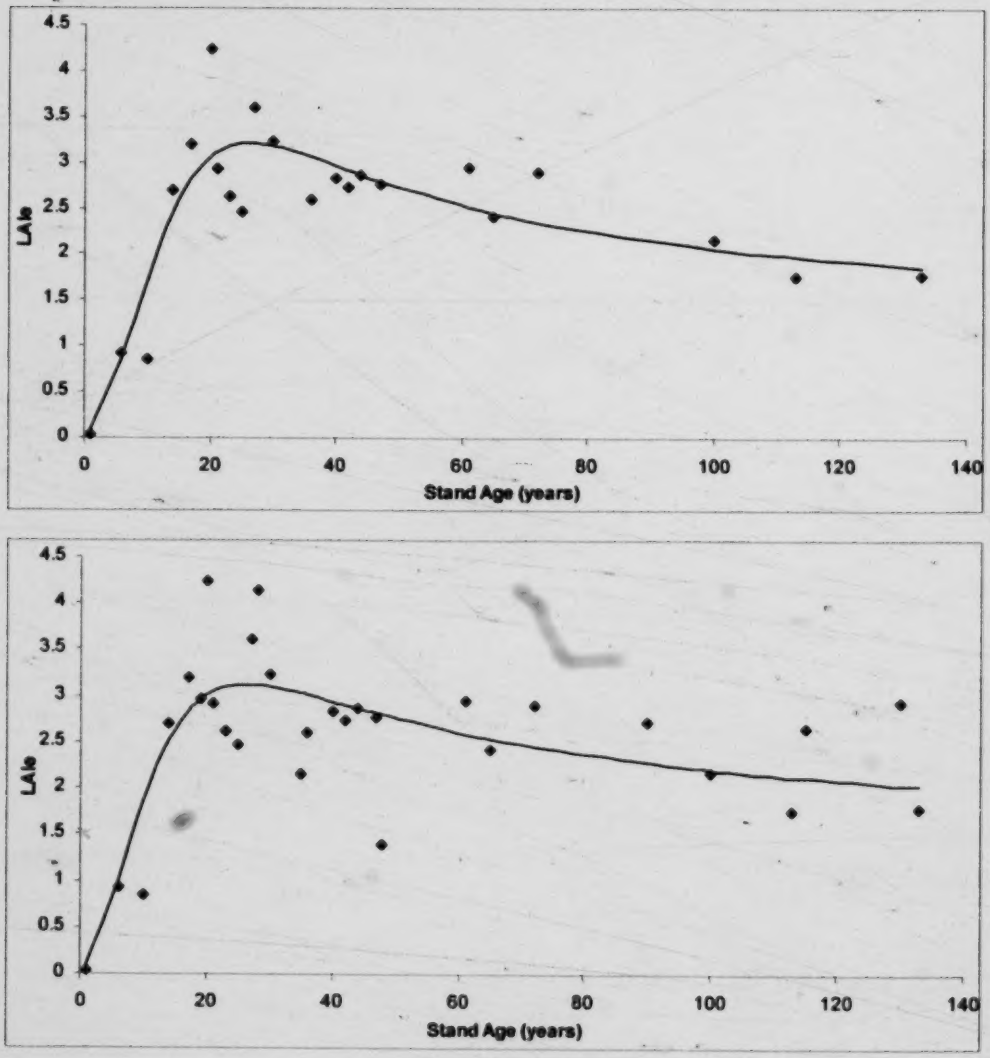


Figure 2-6 Relationship between stand LAIe and total stand sapwood area for all stands (n=28)

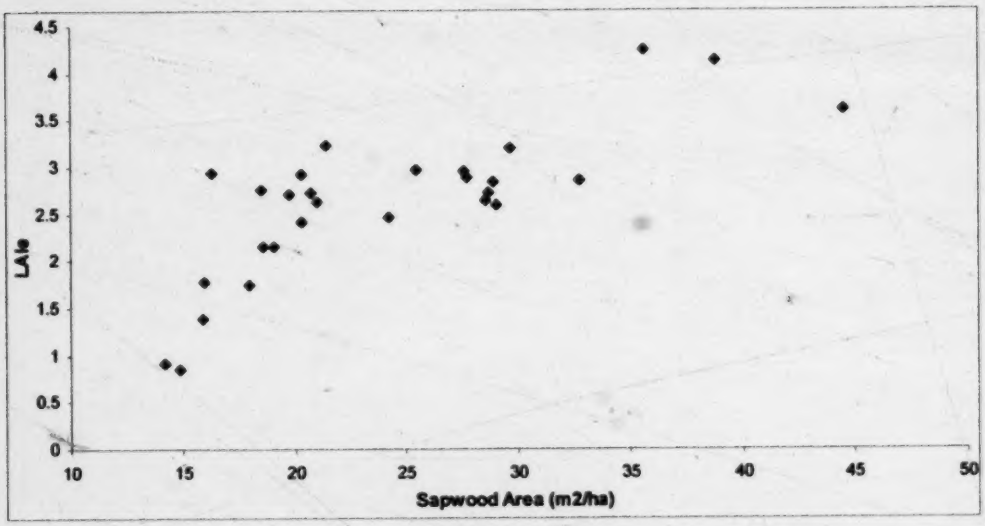


Figure 2-7 Relationship between stand-level LAIe-sapwood area ratio and stand age (years) for all stands (n=28).

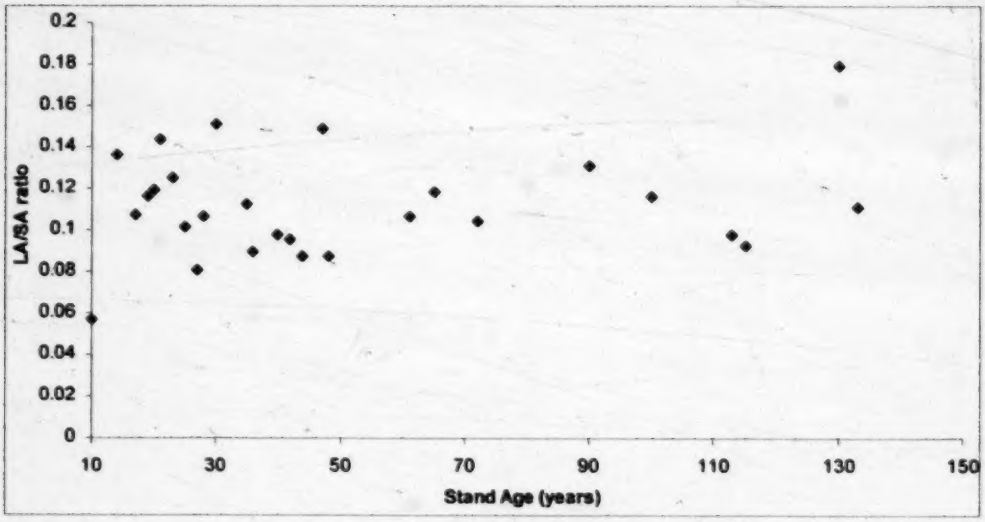


Figure 2-8 Relationship between the stand-level LAIe-sapwood area ratio and stand density for all stands (y=-5E-07x + 0.1177) (r^2 = 0.148, p=0.0432, n=28).

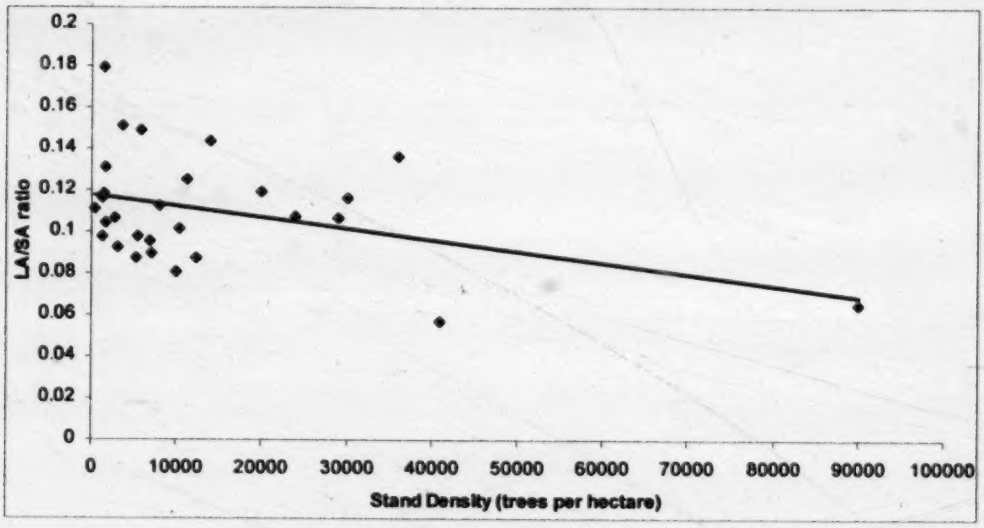
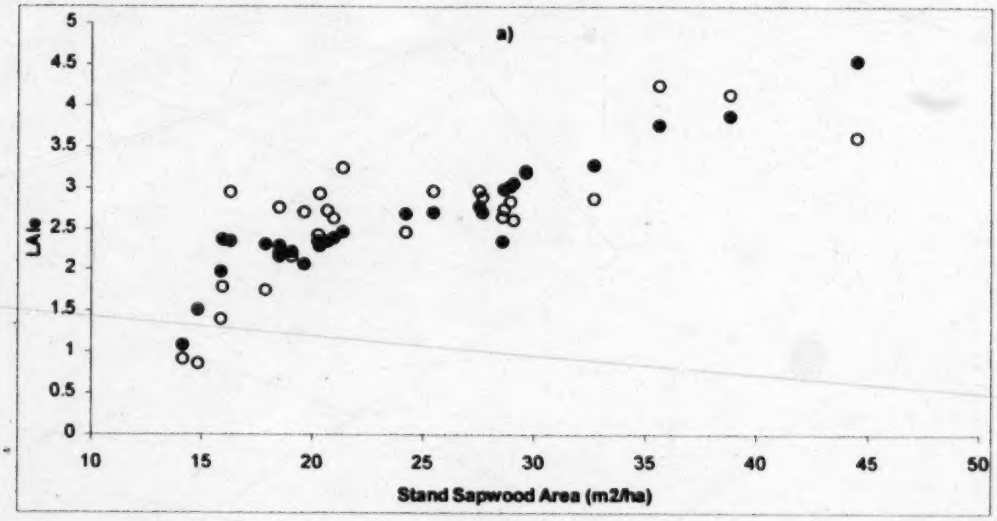


Figure 2-9a) A non-linear multiple regression model to characterize the relationship between stand-level LAIe and stand sapwood area (○) indicates actual LAIe, and (●) indicates LAIe predicted by the model y= -0.00000707(D) + 0.019344(A) – (0.00099(A*S)) + 0.118311(S), where D=stand density(trees/ha), A= stand age (years), and S= sapwood area (m2/ha), b) Scatterplot indicating the relationship between observed LAIe (LAI-2000) and predicted LAIe using the model above (Figure 2-9a) (y=0.7249x + 0.7063 (r^2= 0.667, p<0.0001, n=28)).



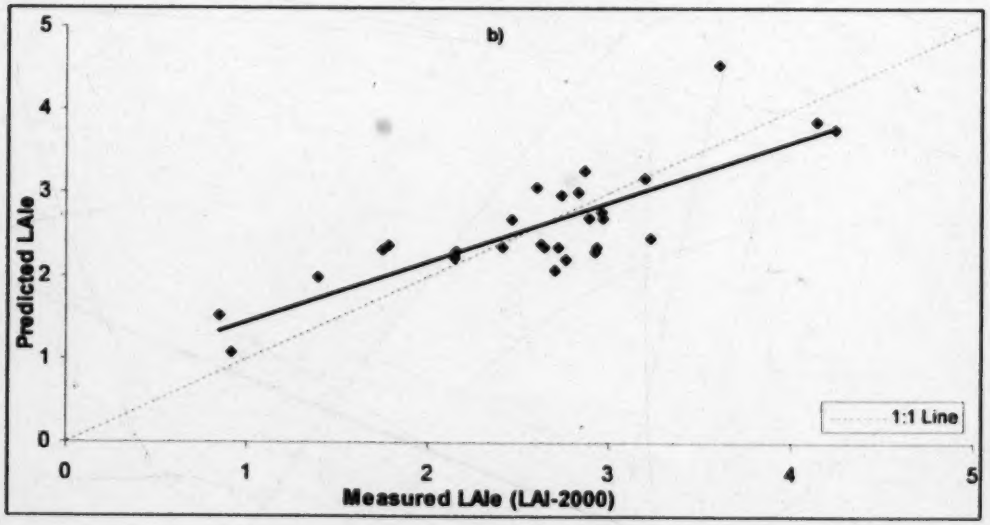
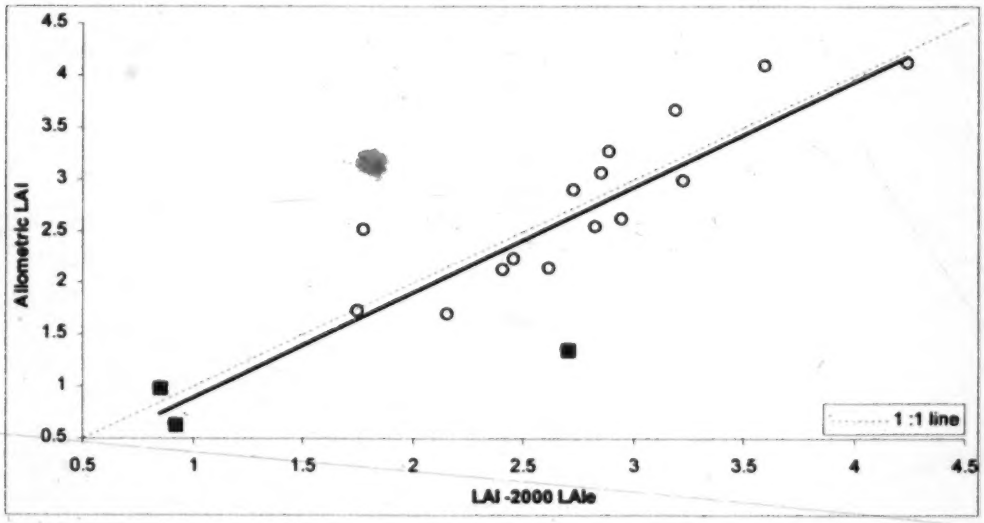


Figure 2-10a) (Top) Relationship between measured LAIe with the LAI-2000 and LAI derived from allometric equations (Long and Smith, 1988 (○) and Dean and Long, 1986 (■)) using sapwood area and distance to the center of the live crown to predict LAI for stands >=18 S.I. (y=1.0134x -0.1236), (r^2=0.7696, p<0.0001, n=18), and b) (Bottom) Relationship between measured LAIe with the LAI-2000 and LAI derived from allometric equations (Long and Smith, 1988 (○) and Dean and Long, 1986 (■)) using sapwood area and distance to the center of the live crown to predict LAI for all stands (y=0.9134x + 0.0324), (r^2=0.6567, p<0.0001, n=24).



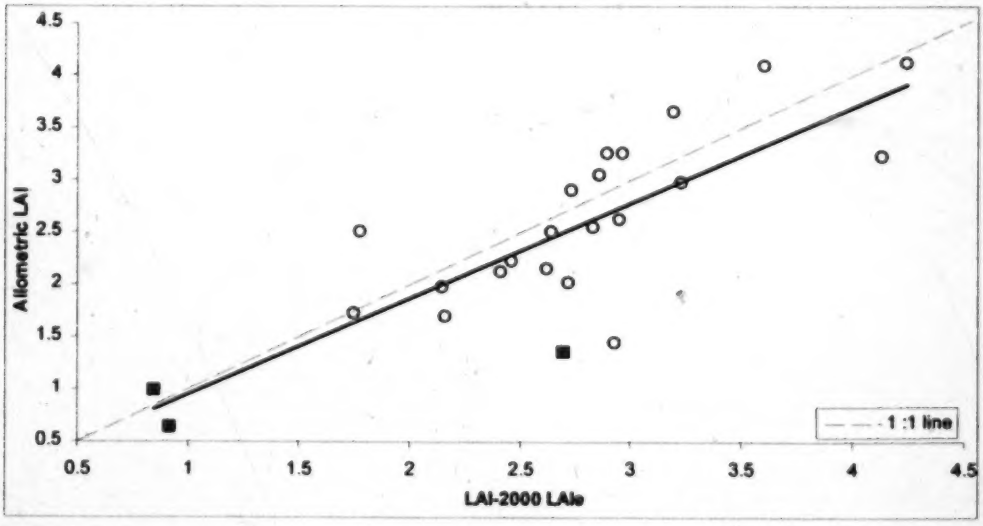


Figure 2-11 The residuals (observed with the LAI-2000 minus predicted using allometric) of LAIe with respect to site index, (○) Long and Smith 1988 < 18m S.I (●) Long and Smith > 18m S.I., and (■) Dean and Long 1986) (y=-0.0695x + 1.5446), (r^2=0.0827, p=0.173, n=24).

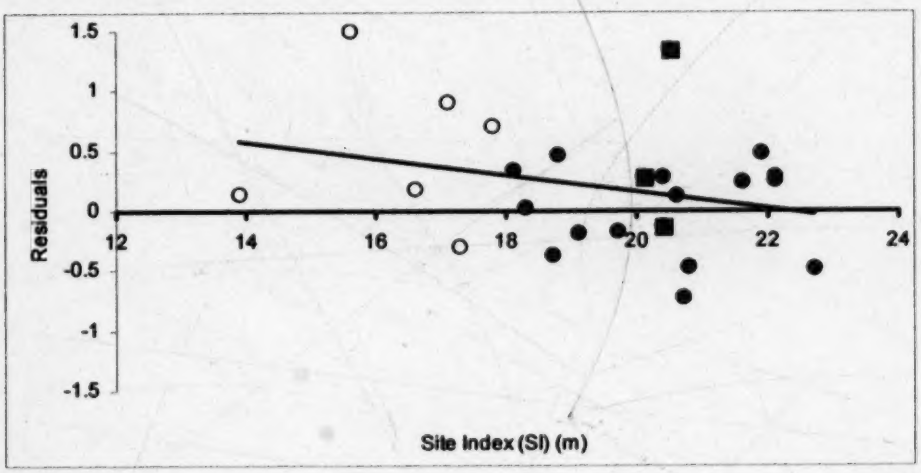
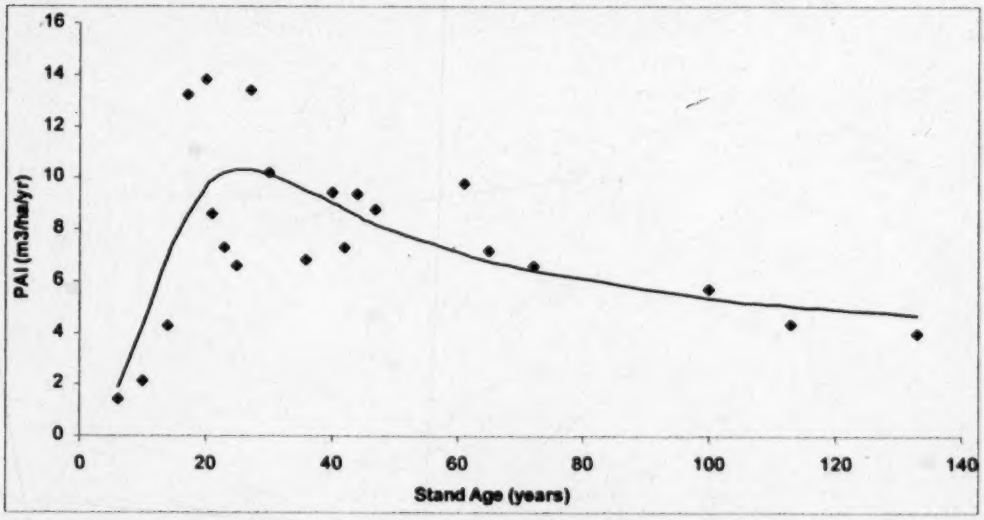


Figure 2-12a) (Top) PAI/age relationship for stands >= 18 SI. Where PAI (m3/ha/yr) (y) = x / (α + β(x) + γ ($\sqrt{}$ (x)), and α = 9.6042, β = 0.4690, and γ = -3.7805 (r^2 =0.558 p<0.0001, n=21), and b) (Bottom) PAI/age relationship for stands all stands. Where PAI (m3/ha/yr) (y) = x / (α + β(x) + γ ($\sqrt{}$ (x)), and α = 9.0462, β = 0.4624, and γ = -3.616 (r^2 =0.526, p<0.0001, n=28).



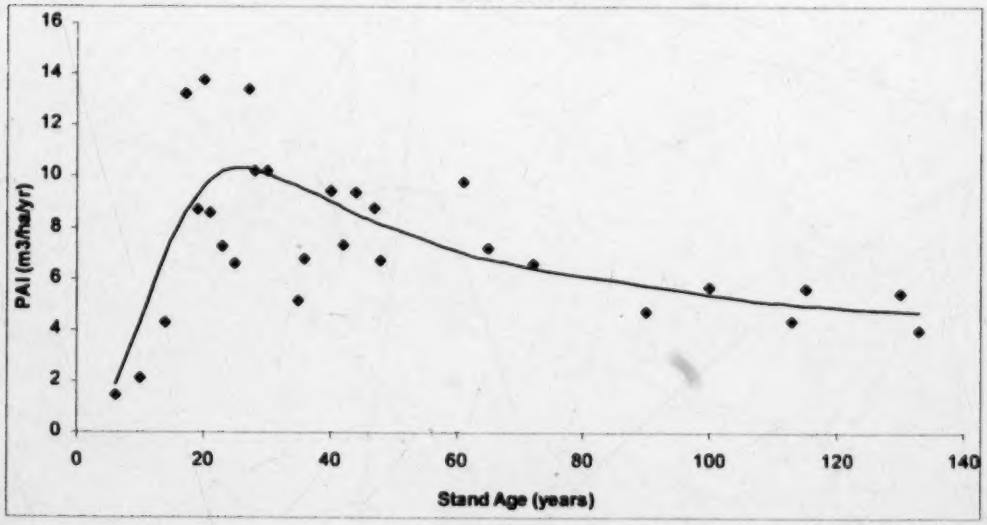


Figure 2-13 Relationship between LAIe and PAI (m3/ha/year) for stands >= 18 S.I. (▲) (y=0.2102x + 0.9908) (r^2 = 0.8307, p<0.0001, n=21), and stands with site index less than 18 (○) (y = 0.2073x + 1.0911, r^2= 0.6796, p<0.0001, n=28).

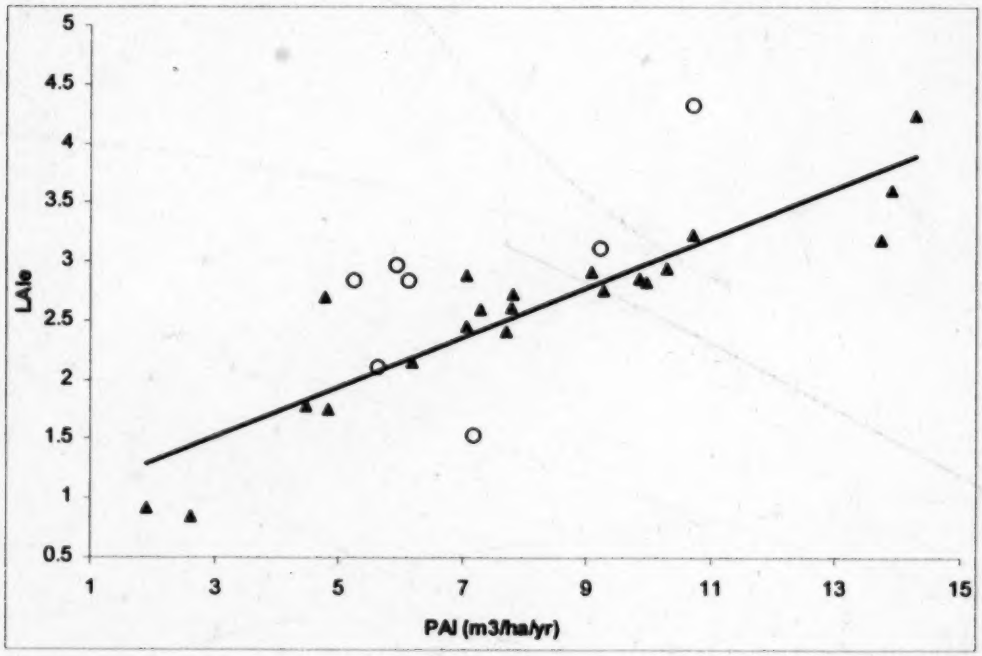


Figure 2-14 Relationship between stand-level growth efficiency ((m3/ha/yr)/LAIe) and stand age for all stands. Where: $y = x / (\alpha + \beta(x) + \gamma(\sqrt{(x)})$, and $\alpha = 9.9057$, $\beta = 0.6904$, and $\gamma = -3.8421$, ($r^2 = 0.31$, $p < 0.0001$, $n = 28$).

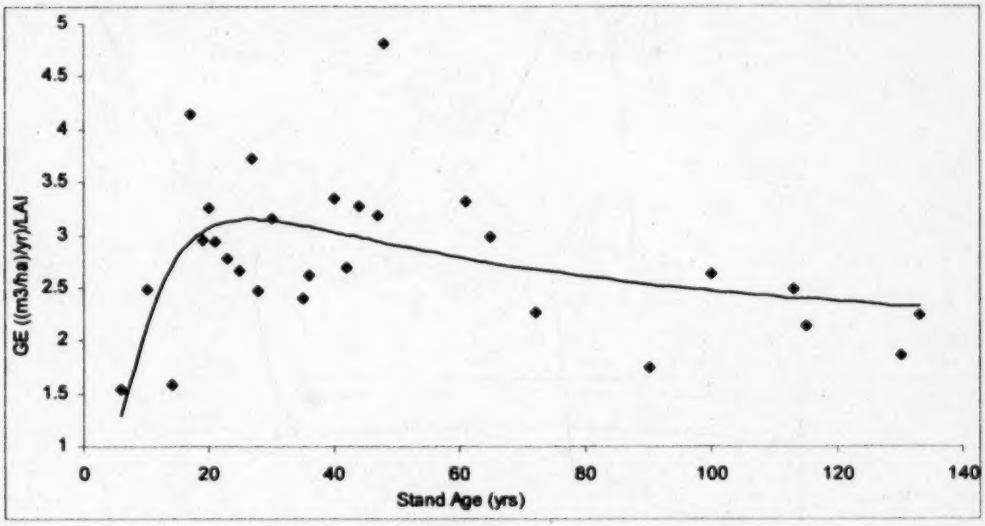


Figure 2-15 Relationship between stand density and average live crown length for all stands ($y=390.73x^{-.05265}$, $r^2=0.945$, $p<0.0001$, $n=28$) (note: axes are on a log scale).

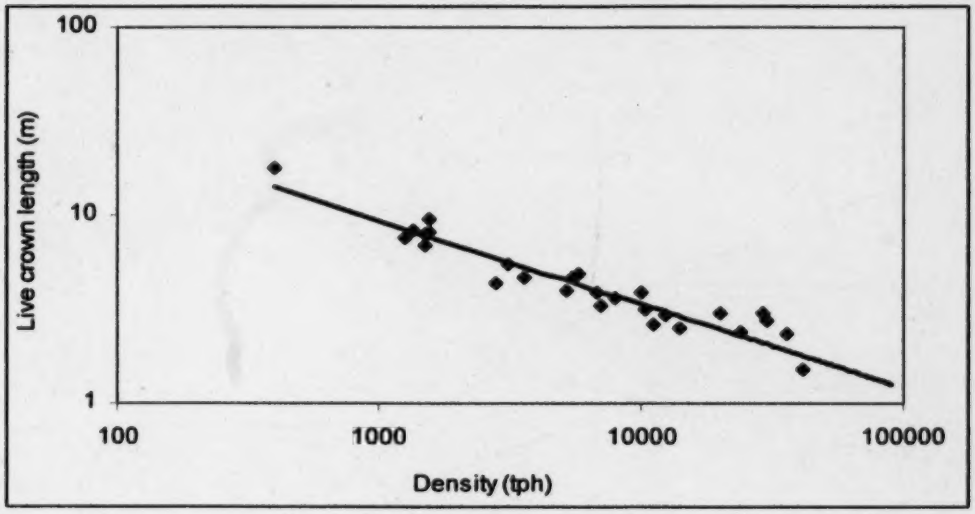
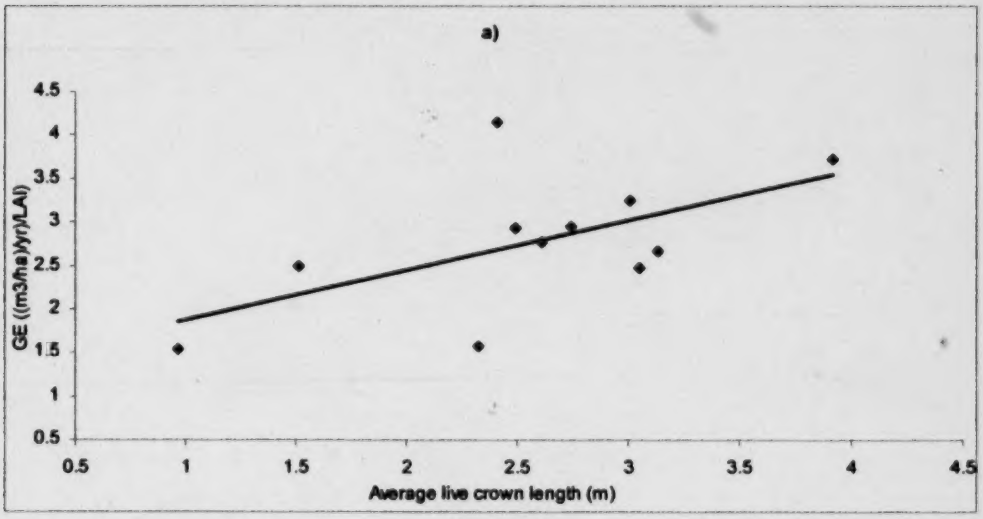
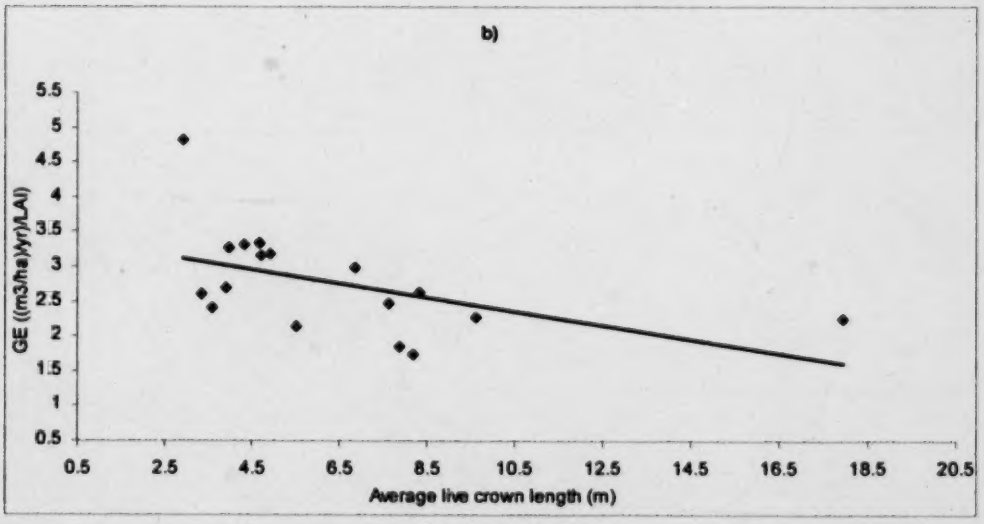


Figure 2-16a) (Top) Relationship between growth efficiency and average live crown length (m) for stands <30 years old (y = 0.572x + 1.3116), (r^2=0.34, p=0.06, n=11), and b) (Bottom) Relationship between growth efficiency and average live crown length (m) for stands >=30 years old (y = -0.1855x + 5.4038), (r^2=0.24, p=0.04, n=17).





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Chapter 3

Rainfall interception Dynamics of Lodgepole Pine

Introduction

Rainfall interception is the fraction of gross precipitation that is captured by vegetative and soil surfaces and subsequently re-evaporated to the atmosphere; thus interception can be considered a net loss of available moisture from the forest. Interception is an important component of the water balance in forests and can account for 10-50% of total annual precipitation (Klaassen et al. 1998). Along with transpiration, interception losses by vegetation can have a major influence on soil moisture and groundwater recharge which, in turn, largely regulate runoff dynamics (including magnitude of peak flow events) and production of water from forested landscapes. However, despite the importance of interception as a major component of forest water balance, surprisingly little research has been conducted on relationships between interception losses and forest canopy condition (species composition or developmental stage) to enable broader characterization or prediction of this water balance component across variable temporal or spatial scales.

Historically, rainfall interception research has been conducted in two main categories; 1) simple empirical description of interception in a rather narrow range of stands or stand conditions, and 2) process based interception modeling most often focused on description of water accumulation and subsequent evaporation dynamics from foliage. Research in the first category has most often described interception losses in stands with specific attributes (i.e. fixed species composition, height, density, diameter range, crown closure). Interception (% of total precipitation) for a range of North American conifer species has been reported to vary from 57% for a large (70m tall, 240 yr old) Douglas-fir stand (McMinn 1960) to 14 % for a mid-rotation (46 yr old) red spruce stand (Mahendrappa and Kingston 1982). Although meta-analysis of interception literature confirms higher interception losses in spruce-fir canopies than in pines (McMinn 1960, Frechette 1969, Mahendrappa and Kingston 1982, Plamondon et. al. 1982, and Valente *et* al. 1997) these estimates come from a variety of stands of variable age, density, species composition, and climatic regions which severely limits the predictive inferences that can be drawn from such analysis. Similarly, early empirical efforts aimed at predicting the change in interception losses in similar stands of variable density (Helvey 1967; Wilm and Dunford 1948)

did not use stand attributes as scalars (independent variables) to enable scaling interception estimates to other stands. As a consequence, the results of these studies are often only applicable to stands with the same attributes and growing under the same climatic conditions as those in these studies.

More recent process focused interception research often use estimates of canopy storage (S) (i.e. the amount of moisture that can be held by a forest canopy) in formulation of interception models (Davie and Durocher 1997; Calder, 1986; Gash, 1979; Rutter et al. 1971). However, these efforts also do not allow for broad prediction or scaling since S is typically expressed in terms of canopy closure or cover density for specific stand structures and species composition. In addition, these physically based models often focus on interception mechanisms, assuming canopy conditions remain constant over time, which makes their application at different spatial and temporal scales difficult.

Canopy leaf area is the principle biological feature of forests that interacts with climate to control the water balance of forests through the regulation of interception and transpiration. The leaf area of forests is also the principle forest attribute driving growth, productivity, and forest succession processes. Therefore leaf area is an important link between forests and their water balance, because spatial and temporal variation in leaf area regulates how climate, disturbance, and successional processes affect the hydrology of forested landscapes. More recent interception models (van Dijk and Bruijnzeel, 2001; Hedstrom and Pomeroy 1998) are beginning to utilize the relationship between S and leaf area index (LAI) in an attempt to make their models robust to different vegetation types or changing vegetation conditions over time and space. However, because these have been validated only with a small set of experimental observations from a very limited set of vegetation types (mostly in agricultural crop species) the broad applicability of such models or use of LAI as a robust scalar for interception in forest vegetation remains uncertain. Conceptually, the relationship between LAI and S is likely to be species specific due to differences in leaf shape, texture as well as branch and twig inclination among tree species. Furthermore, LAI alone may not be strongly sensitive to differences in canopy characteristics such as bole or branch surface area, crown length or tree height that are important in regulating the process of rainfall capture, storage, and evaporation.

The primary goal of this study was to determine whether rainfall interception processes measured at the tree or stand level can be adequately described using fundamental canopy or stand attributes in order to provide the basic tools required to scale interception processes to the landscape level. Specific study objectives were to determine if stand LAI is a sensitive predictor

of differences in rainfall interception losses along a gradient of stand ages/developmental sequences in lodgepole pine. A related objective was to determine if other commonly measured stand metrics typically included in forest stand inventories can be used to scale rainfall interception either alone or in combination with LAI. This should allow for broader extrapolation of interception results in addition to providing forest managers with insight into how one important component of forest water balance is likely to change as forests establish, mature, and age.

Materials and Methods

This study was conducted in even-aged managed and unmanaged lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) stands in the west-central portion of Alberta, Canada in Natural sub regions 10 (Upper Foothills) and 11 (Lower Foothills). All stands within each sub region were located on "d" and "e" eco-sites (Archibald et al., 1996; Beckingham et al., 1996). Stands were located in the region west of Lodgepole (Fig 3-1) within 3 FMA's (Forest Management Areas), including Weyerhaeuser Ltd, Sundance Forest Products Ltd., and Weldwood of Canada Ltd. The region ranges in elevation from 920m to 1100m. Mean monthly temperatures for January and July are approximately –12°C and 15°C, respectively, and average annual precipitation for the region ranges from 540 to 640mm, with approximately 370mm to 450mm falling as rain (Environment Canada, 2002). This region experiences numerous convective-type rainfall events (thunderstorms) throughout the summer months.

Site Selection

Five stands representing a range of stand ages (30-115 years old) and leaf area index (LAI) (1.8-3.2) were selected for interception measurements. Only fully stocked (full site occupancy), pure (90% or greater) lodgepole pine growing on good sites (>16 site index (SI) at reference age 50yrs) (Huang et al. 1997) were selected. Other minor species present in the stands included trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marsh.). Potential stands were identified using age class distribution maps for lodgepole pine provided by the various forest companies as well as digital maps containing site quality information. In addition, potential stands could not contain visual indicators of insect or disease attacks that might affect LAI. Although some stands contained a mixture of species, rainfall interception processes were measured within regions in the stand that were dominated by 100% lodgepole pine. For a more detailed description of the site selection process, as well as the volume growth and LAI sampling procedures please refer to Chapter 2.

Interception Measurements

Rainfall interception was measured indirectly by measuring the difference between gross precipitation (above or outside the stand) and throughfall + stemflow (below the canopy) as follows (Equation 3-1):

Equation 3-1 $I = Pg - (TF + SF)$

Where: I is the rainfall intercepted by the canopy (mm), Pg is the rainfall (mm) occurring at the site (gross precipitation), TF is throughfall (mm), and SF is stemflow (mm). Tipping bucket raingauges were used to measure gross precipitation and throughfall on a rainfall event basis. The amount of rainfall intercepted was calculated for each rainfall event. In order to accurately estimate the interception storage capacity of each stand it was necessary to ensure interception estimates for each event began with a canopy that was completely dry (i.e. independent estimates of interception for each rainfall event). Independent rainfall events were defined as being preceded by at least a 4-hour precipitation-free or dry antecedent period (as measured by lack of precipitation the open precipitation gage). Choosing an overly long dry antecedent interval as the minimum event separation criteria would result in classification of fewer discrete events and would therefore unnecessarily reduce the sample size. Conversely, choosing an overly short interval could result in only partial canopy drying between events leading to an underestimate of interception storage capacity. Iroumé and Huber (2002) used a 5 hr antecedent dry period for their study in Chile, while Klaasen et al. (1998) used a 2 hr antecedent dry period for their study in the Netherlands. The 4-hour period dry antecedent interval criterion selected for this study represented a balance between these two factors and is generally consistent with criteria used by other researchers to define isolated rainfall events.

Summer 2003

During the summer of 2003, gross precipitation and throughfall volumes were measured in five stands; three in sub region 11 and two in sub region 10. Stemflow was considered negligible (equal to zero) for 2003. Throughfall was measured with a series of randomly-located tipping bucket raingages located within the tree volume growth sampling plots (refer to Chapter 2). Gross precipitation was measured with one tipping bucket raingage located in an adjacent opening. All of the tipping bucket gauges were equipped with HOBO Event Loggers (Onset, 1999).

Three of the stands were equipped with 4 throughfall gages and two stands had 3 gages. Gage allocation was based on the size of the tree volume sampling plot (e.g. the smaller plots had 3 gages) and the limited number of gages available. Each throughfall and open gage was equipped with a v-notched galvanized steel trough (152.4 cm long by 19.5cm wide) to increase the size of the catch surface area thereby reducing some of the spatial variability in throughfall. The throughfall troughs were located 50cm above the ground and the open troughs were located 150cm above the ground. The troughs were tilted (~10%) in order to capture throughfall and divert it to the gage. Each gage was covered with an inverted 5-gallon pail to prevent throughfall from entering the gage directly. The end of each trough was fitted with a plastic funnel and a 19mm hose that deposited throughfall collected from the trough through the funnel, hose, pail, and into the gage. Each hose was fitted with a screen to prevent debris from entering and plugging the gage orifice (Figures 3-2a-b).

Because different tipping bucket raingages were used to collect gross precipitation and throughfall volumes, individual raingages were calibrated as detailed in Appendix 3-1. Once individual gages were calibrated, it was necessary to convert the known volume per tip to an areal-basis (mm), so that comparisons between gross precipitation and throughfall could be made. For each rainfall event, average throughfall was determined by taking the average of all throughfall gages in each stand.

Summer 2004

After analyzing the precipitation and throughfall data from the 2003 field season, it became clear that the original assumption of negligible stemflow during rainfall events in the study region was likely not a valid assumption. A second field season was needed to measure throughfall and stemflow concurrently and collect data on how these processes varied by event size to enable post-hoc correction of interception data from the 2003 field season. During the summer of 2004, throughfall and stemflow was measured in two of the same five stands measured in 2003 (one in sub region 10 and one in sub region 11) using the same procedures outlined above. In each stand, throughfall was measured with four randomly-located raingages, and gross precipitation with one raingage located in an adjacent opening (all gages were equipped with troughs and inverted pails as above).

Stemflow

Stemflow was measured at 1.3m on 2 trees with different diameters in each stand. Each tree was wrapped 1.5-2 times with a semi-circular (split) 19mm hose and attached to the tree with 9/16 inch staples. Prior to attaching the hose, any loose bark was removed and the surface smoothed with and axe. The junction between the hose and the tree was sealed with silicone to prevent stemflow from by-passing the hose. Each tree was fitted with a plastic collar that shielded the hose from direct precipitation from above to limit stemflow measurements only to water traveling down the bole. The plastic collar was attached to spacers designed to anchor the collar and to maintain a gap between the collar and the bole. Stemflow was measured with tipping bucket raingages (one per tree). Each gage was covered with an inverted 5-gallon pail to prevent throughfall from entering the gage. A 19mm hose diverted collected stemflow through the top of the pail and into the raingage (Figure 3-3a-b)

Scaling stemflow volume from the tree to the stand level

The same procedure for calibration was carried out for all tipping bucket raingages used to measure stemflow volume. However, a different approach was required to convert stemflow volumes to an areal-based measurement so that gross precipitation, throughfall, and stemflow could be compared.

Total stemflow volume per tree was determined for each rainfall event that generated stemflow. A unique linear relationship (i.e. regression slopes and intercepts) between stemflow volume and rainfall event size was determined for each of the four sample trees in the two stands. Next, it was necessary to find a tree attribute that was related to the rate at which stemflow volumes were generated with increasing event size to enable scaling of the unique slopes/intercepts from the 4 individual trees to all trees in the plots. Both basal area (BA) (Crockford and Richardson, 1990a), and crown projection area (Herwitz and Levia, 1997) have been used to scale stemflow generated from sample trees to all trees within a particular stand. However, problems arise when scaling the results among stands because BA masks differences in stem diameter distribution, and branch/canopy structure among stands while crown projection area is generally not measured as part of forest inventories thus limiting its value as an independent variable for scaling. I chose an approach using easily measured stand attributes that characterize the stemflow process.

Stemflow is generated when rain falls on the vegetative portion of the tree (leaves or bole), coalesces and flows down the bole where it will eventually reach the ground. Conceptually,

the amount of stemflow generated for a stand is a function of the aggregated individual tree sizes. While the random orientation of leaves within crowns acts to capture rainfall, the vertical orientation of boles acts to both transport and store water (water adhering to bark during downward transport) draining from the crown. As these attributes are roughly described by individual tree height and diameter, these were chosen as the independent variables to scale stemflow volume for trees of variable size among different event sizes. This approach is supported by studies reporting positive correlations between stemflow production and tree basal area (represented by tree diameter) (Crockford and Richardson, 1990a, 2000), as well as stem length (Martinez-Meza and Whitford, 1996). De Ploey (1984) included mean tree diameter and height as model parameters describing the stemflow generation process of birch trees. Although the stemflow generation process is quite complex, tree height and diameter affect the production of stemflow in several key ways. In general, as tree height increases, there is more surface area to store intercepted rainfall, however, taller trees also present a larger surface to catch rain falling at oblique angles, in addition, taller trees also have a longer path length for stemflow to travel before it is measured (usually at the base of the tree), which would result in a delayed response. Similarly, as tree diameter increases, there is a larger surface area to store intercepted rainfall; however, larger diameter trees also present a larger surface to catch rain falling at oblique angles. In addition as with many other species, larger diameter (older) lodgepole pine trees tend to have thicker, rougher bark than smaller diameter (younger) lodgepole pine trees, as a result, they tend to store more rainfall and generate less stemflow than their younger counterparts.

As a result, the slopes from the linear regressions of the stemflow volume by rainfall event size (mm) relationship from each of the four sample trees were then regressed against the height (m) and diameter (cm) for each tree using a multiple regression approach. Similarly, the intercept (minimum event size or threshold event required to generate stemflow) was regressed against the height (m) and diameter (cm) of all four trees using multiple regression. The resulting relationships between regression slopes with height and diameter and between threshold event size with height and diameter were used to predict both the threshold event size for stemflow generation and subsequent stemflow volume by event size for each tree in all five stands.

Stemflow volume (mm^3) by event size (mm) was converted to an areal-based measurement (mm) by summing the predicted volumes for all trees in the volume sampling plot and dividing by the total plot area (mm^2).

Interception storage capacity (S)

Rainfall interception in all stands was calculated for each event in both years using Equation 3-1. Interception in 2004 was determined using measured gross precipitation, throughfall and stemflow, while interception in 2003 was determined using measured gross precipitation, throughfall and post-hoc estimation of stemflow (as outlined above).

The interception storage capacity for each stand was determined from the relationship between total rainfall interception (mm) and the rainfall event size (mm). S was estimated for each stand using the Ratkowsky, (1990), non-linear model:

Equation 3-2 $y = \alpha - \beta\gamma^{x}$

Where y = the predicted rainfall interception (mm), α is the horizontal asymptote corresponding to $X \rightarrow \infty$ (S in mm), β is the range of the response between X=0 and X=∞, and γ relates to the rate at which y changes from its initial value at x=o, to its final value α (Ratkowsky, 1990).

In order to determine the interception storage capacity of each stand, it was necessary to include only continuous rainfall events. For the purpose of this analysis, I defined a continuous event as one being separated by at least a 4 hour rain-free period (i.e. a discrete event) and having no more than one rain-free period of greater than 1.5 hrs within it. This reduced the effect of evaporation within the event and enabled actual interception storage to be more closely approximated.

Results

Stand Characteristics

The five stands selected for interception measurements spanned a range of ages and developmental stages. Stands ranged in age from 30-115 years. Three of the five stands were of fire origin and two were artificially regenerated using drag scarification (Table 3-1). Stand density in the artificially regenerated stand was similar to densities expected after a fire, and high enough to be considered full site occupancy. Stand densities ranged from 1250-7000 trees per hectare and generally co-varied negatively with stand age. Although the objective was to sample "good" site quality stands (SI>16 m), because of logistical limitations, one site (Owl-9) having an SI of 13.9 was included in the measurements. The SI of remaining four sites were above 18 m.

Average stand heights ranged from 9.1m to 20.6m at 35 and 113 years respectively, and average stand volumes ranged from 134.5m^3/ha at age 30 to 495.3m^3/ha at age 113. The mean stand basal area for all 5 stands was 39.9 m^2/ha (s.d. 8.75 m^2/ha), and ranged from 24.9m^2/ ha at age 30 to 45.8m^2/ha at age 115 (Table 3-1). The average stand-level effective leaf area index (LAIe) (refer to Chapter 2) ranged from 1.75-3.23 (s.d. 0.556) using the LAI-2000.

Gross Precipitation and Throughfall

During the summer of 2003, between 27 and 51 rainfall events were recorded for each of the five stands (Table 3-2). Measured gross precipitation for the summer (Mid June-Mid October) ranged from 132.0mm for OWL 9 to 51.7mm for BR 1. Total summertime throughfall ranged from 81.8mm to 34.0mm for the same two stands. Throughfall accounted for between 61.8% and 65.8% of gross summer precipitation across the five study sites.

During the summer of 2004, 21 and 39 rainfall events were recorded at the PC 1 and ER 1 sites, respectively during the period June 5-July 14. Gross precipitation was 90.8mm for PC 1 and 169.9 for ER 1 and throughfall was 67.6mm and 114.2mm, representing 74.4% and 67.2% of gross summer precipitation, respectively (Table 3-2). Although the total number of rainfall events varied between stands, most of the events occurring at these sites were small (<2.5mm) and of short duration (Figure 3-4a-e). However, larger events in excess of 11mm were recorded at all sites.

Stemflow

Because bark/bole storage of water reduces stemflow by a small amount during rainfall events, only a sub-sample of the total rainfall events measured during the summer of 2004 were large enough to generate stemflow. Only 8 of the 21 events generated measurable stemflow at the PC 1 site, and 11 of the 39 events (7 for tree #20 and 11 for tree #1) generated stemflow at the ER 1 site. For each tree at the PC 1 site, very strong linear relationships were evident between the volume of stemflow collected and size rainfall event that generated the stemflow (r^2=0.93, $p<0.0001$ for tree #1, and r^2=0.98, $p<0.0001$ for tree #20) (Figure 3-5a). The trees at the ER 1 site also showed strong linear relationships between the volume of stemflow collected and size rainfall event that generated the stemflow (r^2=0.84, $p<0.0001$ for tree #1, and r^2=0.603, $p=0.003$ for tree #20) (Figure 3-5b) However, these relationships were unique for each individual tree and between the two stands. The threshold event size (the event size required to generate stemflow as quantified by the x-intercept) also varied by individual trees, but was less than 2.7mm for the

smaller PC 1 trees, while the threshold for the larger ER 1 trees was greater than 5.5mm (Table 3-3). Within each of the PC 1 and ER 1 sites, stemflow volume was greater for the larger diameter (basal area) trees for a given event size. However, across sites, the smaller diameter trees of PC 1 generated more stemflow than the larger diameter trees of ER 1 for a given event size.

The relationship of the slopes from the linear regressions between stemflow volume and rainfall event size with individual tree basal area (r^2=0.201, p=0.55) and leaf area (r^2=0.006, p=0.92) did not provide adequate predictive power to support scaling stemflow relationships to other stands (results not shown). However, adequate relationships between the slopes of the stemflow volume/rainfall event size relationship (slope) and the tree heights (m) and diameters (cm) of the four sample trees were observed (Equation 3-3).

Equation 3-3 Slope = -84.06(ht) + 56.95(dia) + 640.06 (r^2=0.988, p=0.006)

A similar relationship was observed between the threshold event size (mm) required to generate stemflow and the heights (m) and diameters (cm) of the sample trees (Equation 3-4).

Equation 3-4 Threshold event size (mm) = 0.419(ht) - 0.195(dia) +1.31 (r^2=0.985, p=0.008)

Predicted stemflow (stand level)

The resulting relationships between slope and threshold event size with tree height and diameter were used to scale stemflow volume to the stand level by applying linear equations (3-3 and 3-4) to each tree in the volume sampling plots in all five stands. Stemflow volume (mm^3) by event size (mm) was converted to an areal-based measurement (mm) by summing the predicted volumes for all trees in the volume sampling plot and dividing by the total plot area (mm^2). Consistent with measured stemflow at the tree scale, strong positive linear relationships were evident between predicted stand level stemflow responses to increasing event size (Figure 3-6). Predicted stand-level stemflow also varied considerably among stands. In general, for a given event size, stemflow was highest for PC 1, followed by OWL 15, BR 1, ER 1, and OWL 9. The percentage of gross precipitation occurring as stemflow ranged from 9.3% for PC 1 to 1.0% for ER 1, and threshold event sizes (size of event required to generate stemflow) ranged from 3.0 mm for OWL 15 to 5.2mm for OWL 9 (Table 3-4a).

Rainfall Interception Storage Capacity

Average total seasonal rainfall interception (mid June - mid October) corrected for stemflow (total interception = gross precipitation – (throughfall + predicted stemflow)) during

2003 and 2004 varied considerably among the five study stands (Table 3-4b). Although total interception losses varied between 14.3 and 86.1mm among stands, rainfall interception as a percentage of total gross precipitation was more similar among stands (23%-37%). Rainfall interception losses generally accounted for most of the total gross precipitation for the smallest rainfall event sizes and the percent interception losses declined sharply as rainfall event size increased. Rainfall interception expressed as percent of gross precipitation exhibited a negative exponential relationship with event size for all stands (Figures 3-7a-e).

Total stand interception storage capacity was determined from the asymptotic relationship between rainfall interception (mm) and rainfall event size as indicated by the value of the horizontal asymptote (α) in Figures 3-8a-e. As a result, S varied between 1.06 and 3.96 mm among the five stands (Table 3-4b). However, relationships between S and stand LAIe, stand basal area, and the total stand bole surface area were generally weak (not significant at α=0.05). Furthermore, interception storage capacity was negatively related to stand LAIe (r^2= 0.538, p=0.158), while positive correlations were observed for stand basal area (r^2= 0.692, p=0.08) and stand bole surface area (r^2= 0.412, p=0.243). However, a stronger relationship between S and total stand volume was evident (r^2= 0.906, p=0.013) (Figure 3-9).

Discussion

The results from this study indicate that the effective leaf area index (L_eAIe) may not be the most important stand attribute regulating rainfall interception in lodgepole pine forests. Other stand metrics may provide greater potential for both predicting and scaling rainfall interception.

Throughfall and Stemflow

Although total throughfall (mm) varied considerably between stands, throughfall as a percent of gross precipitation was generally similar for all stands (62%-74%). Though no previous rainfall interception studies (to my knowledge) have been conducted on lodgepole pine, throughfall as a percentage of gross precipitation has been reported to vary from 70-86% in *Pinus radiata* and *P. pinaster* stands of variable density and age by Crockford and Richardson (1990b), Valente et al. (1997), and Loustau et al. (1992). Although these values are slightly higher than the throughfall measured in my study, these other studies were conducted under very different climatic regimes (Chile, France, Australia) and differences in mean rainfall event size among regions alone could produce large variance in throughfall. Other regional climatic factors can also affect throughfall. For instance, the slightly higher throughfall values observed at PC1 and ER1

in 2004 compared to 2003 were likely due to higher rainfall intensities for the storms during 2004. The average storm size was 2.8mm, and 4.3mm for PC1 in 2003 and 2004 respectively, and 1.8mm and 4.4mm for ER1 in 2003 and 2004 respectively. Crockford and Richardson (2000) and Herwitz (1997) suggest that high intensity rainfall events may produce branch flow that exceeds the capacity of flow paths resulting in dripping and greater throughfall in higher intensity storms of similar total size.

Throughfall was not strongly affected by variation in stand characteristics along the age gradient in my study. For instance, I observed identical throughfall (65.8 % of Pg) at OWL 15 (30 years old) and BR 1(61 years old) despite large differences in mean tree size among these two stands. More importantly and contrary to my expectations, throughfall was also not sensitive to variation in LAIe among stands and was actually negatively (weakly) correlated to stand LAIe. At best, this suggests LAIe alone does not exert strong control over throughfall among the stands I studied. Though undoubtedly LAIe does play a regulatory function in the interception process, the distribution of leaf area in the canopy (i.e. canopy gaps) probably plays an equal or greater role in regulating throughfall than LAIe alone.

Stemflow (SF) ranged from 1.0-9.3% of gross summer precipitation which also compares favorably with stemflow estimates from studies of other pine species (1.3-12.5% of gross precipitation in *Pinus* radiata, *P.* sylvestris, and *P. wallinchiana*) considering such estimates were generated from stands of differing density, age, and climatic regions (Crockford and Richardson 1990a, Langford and O'Shaughnessy 1978, Feller 1981, Smith 1974, Lorens et al. 1997, and Singh 1987). Although stemflow as a percent of gross precipitation can be low, depending on the distribution of rainfall, water intercepted by boles can comprise a large component of overall stand interception since the water-holding capacity of bark is greater than that of foliar surfaces (Herwitz, 1985; Liu, 1998). In this study most of the rainfall events were smaller than the threshold event size required to generate stemflow; between 69% (OWL 15) and 93% (BR 1) of all events recorded during this study were less than the predicted threshold event sizes for these stands. Thus, virtually all of the stemflow observed in this study was generated from a very few large events. While previous researchers have suggested that because SF is generally very low compared to throughfall, this component can be safely neglected in determination of rainfall interception dynamics in some forests (Lankreijer et al. 1999, Klaassen et al., 1998). However, my results illustrate that the variation in stemflow by rainfall event size is a very important component of seasonal rainfall interception dynamics and is particularly important in defining stand-level interception storage capacities (S). For example, when stemflow was neglected in

determining stand interception (I=Pg-TF), the relationships between I and rainfall event size were linear suggesting canopy S was not filled during any of the events I observed, whereas when stemflow was included (I=Pg-TF-SF) the relationships between I and event size were non-linear with a horizontal asymptote corresponding to S. For the five stands in this study, the inflection point I observed in the interception-event size relationships roughly corresponded to the threshold event size required to generate stemflow. Thus because of the strong variability of stemflow with variable event size, failure to account for both the threshold behavior and rapid increase in stemflow during larger events would likely result in inaccurate representation of interception dynamics in general, and overestimation of S in particular.

My results also suggest that basal area (BA) of trees may not serve as either a sensitive independent variable for prediction of SF at the individual tree level nor scaling to plot or stand scales as has been suggested by others (Crockford and Richardson, 1990a). Though inferences that can be supported based on a sample size of 4 trees (measured stemflow in 2004) are admittedly limited, I found total tree height and diameter provided better prediction of SF than using BA as these variables probably more closely describe the stemflow generation process. The size of tree stems (collectively described by height and diameter) regulate stemflow in several ways, though the relationships with tree size do not appear to be a simple linear relationship because some stemflow processes are positively related to stem size while others are not. For instance, stems capture rainfall falling at even slight oblique angles with wind turbulence within canopies (Crockford and Richardson, 1990a; Crockford and Richardson, 2000) and also act to store water on bark surfaces. Both of these functions are positively associated with total bole surface area. However, once bark storage is exceeded, smaller stems have shorter travel distance to the forest floor. In contrast to suggestions by Crockford and Richardson (1990a) my limited results suggest using individual independent variables such as BA or bole surface area do not adequately describe the dynamics of the stemflow process. Furthermore, while scaling stemflow using BA (Crockford and Richardson, 1990a) may be appropriate within a stand, using BA to scale estimates to other stands may lead to erroneous results. I found individual tree size to be an important determinant of stemflow and using total stand BA to scale results among stands may mask differences in tree size distribution since stands with the same basal area may have very different stemflow generation responses to increasing event size (i.e. a stand with 10000 small trees vs. a stand with 200 large trees). Although several studies have used BA (Crockford and Richardson, 1990a; Herwitz and Levia, 1997) or DBH (Feller, 1981) to convert stemflow volume to an areal basis and to scale stemflow from sample trees to the entire stand (Hanachi and Rapp,

1997), my results indicate both height and DBH together provide a better description of the stemflow process to enable scaling.

Interception

Rainfall interception as a percentage of gross precipitation ranged from 23%-37% with corresponding estimates of canopy interception storage (S) ranging from 1 to 4 mm among the stands I studied. Again, though I am unaware of any previous rainfall interception studies in lodgepole pine, my results are comparable to studies conducted on other *Pinus* species. Crockford and Richardson (1990c) report a that a young *Pinus radiata* plantation intercepted 18.3% of gross precipitation (Pg) and with S of 2.4mm; Lankreijer et al., (1999) found that a *Pinus sylvestris – Picea abies* forest intercepted 25.8% of Pg, with a S of 2.5mm, and Llorens and Gallart (2000) found S in their *Pinus sylvestris* stands ranged from 1.24 to 2.65mm in still air and 1.16 to 2.47mm under windy conditions.

Although the S I observed in my stands was not particularly large, the amount of rainfall intercepted by these forests can play a large role in determining the overall stand water balance since most of the rainfall events in this region are less than S. During the summer of 2003 and 2004, between 50% and 85% of all events recorded were smaller than the S of the individual stands resulting in 23% to 37% of total summer precipitation being lost to canopy interception alone. In addition, once the canopy interception storage capacity is exceeded and throughfall and stemflow begin contributing moisture to the forest floor, litter interception becomes important and can severely limit the amount of moisture reaching the soil. Golding and Stanton (1971) found that litter interception for a young lodgepole pine forest in Alberta was 1.8mm/cm of forest floor thickness. Although the forest floor thickness for the stands in this study varied, they were all greater than 2 cm suggesting litter interception for these pine forests may be as important as canopy interception. As a result, it is the relatively infrequent large rainfall events during the summer growing season that are responsible for contributing to soil moisture and groundwater recharge during the period of highest annual precipitation.

Scaling Interception

The primary goal of this study was to determine whether rainfall interception processes measured at the tree or stand level could be adequately described using fundamental canopy or stand attributes in order to provide the basic tools required to begin scaling rainfall interception process to the landscape level. Contrary to my expectations, LAIe was unrelated to both I and S

(weak negative relationship for I and S; r^2=0.53, p=0.17, and r^2=0.54, p=0.16 respectively). This finding is in strong contrast to the many previous studies that argue LAI is good predictor of S in woody plants (Leonard, 1967; Leyton et al., 1967; Rutter and Morton, 1977; Singh, 1987; Gash, 1979) and many related models using LAI to estimate canopy cover fraction and S (van Dijk, and Bruijnzeel 2001, Loustau et al. 1992, Davie and Durocher 1997, Calder, 1986, Gash, 1979, Rutter et al. 1971). While initially surprising, my observation of poor relationships between LAIe and S probably reflected the fact that stands with higher LAIe were younger stands with less surface area in boles as well as having smoother bark. In general, this suggests that LAIe alone does not capture other processes related to stand-level interception dynamics such as role of boles in capture, storage, and transport of water. Although LAIe is undoubtedly a good predictor of interception storage of capacity foliar surfaces, it does not account for the interception storage capacity of boles. I observed that overall stand interception storage capacity was better explained using total stand volume which integrates the roles of height and diameter distribution within my stands.

Conclusions

My results raise some important questions about the broad applicability of recent interception models that use LAI as the basis for estimating stand-level interception storage capacity (S) (Davie and Durocher 1997; Calder, 1986; Gash, 1979; Rutter et al. 1971) In species with relatively small crowns (and perhaps LAIe), rainfall stored by boles may be a more important component of overall stand-level interception storage than rainfall stored by leaves/needles. This suggests that generalized interception models should be modified to include a component of branch and bole storage to produce a more robust prediction of interception dynamics in forests. Furthermore, because I found S to be closely related to total stand volume which is a commonly measured and readily available stand metric, my work suggests stand volume could be used as a suitable independent variable to scale S across spatial and temporal scales in lodgepole pine. This should allow for broader extrapolation of interception results in addition to providing forest managers with insight into how one important component of forest water balance is likely to change as forests establish, mature, and age.

Tables and Figures

Figure 3-1 Map of study area, including rainfall interception stands.

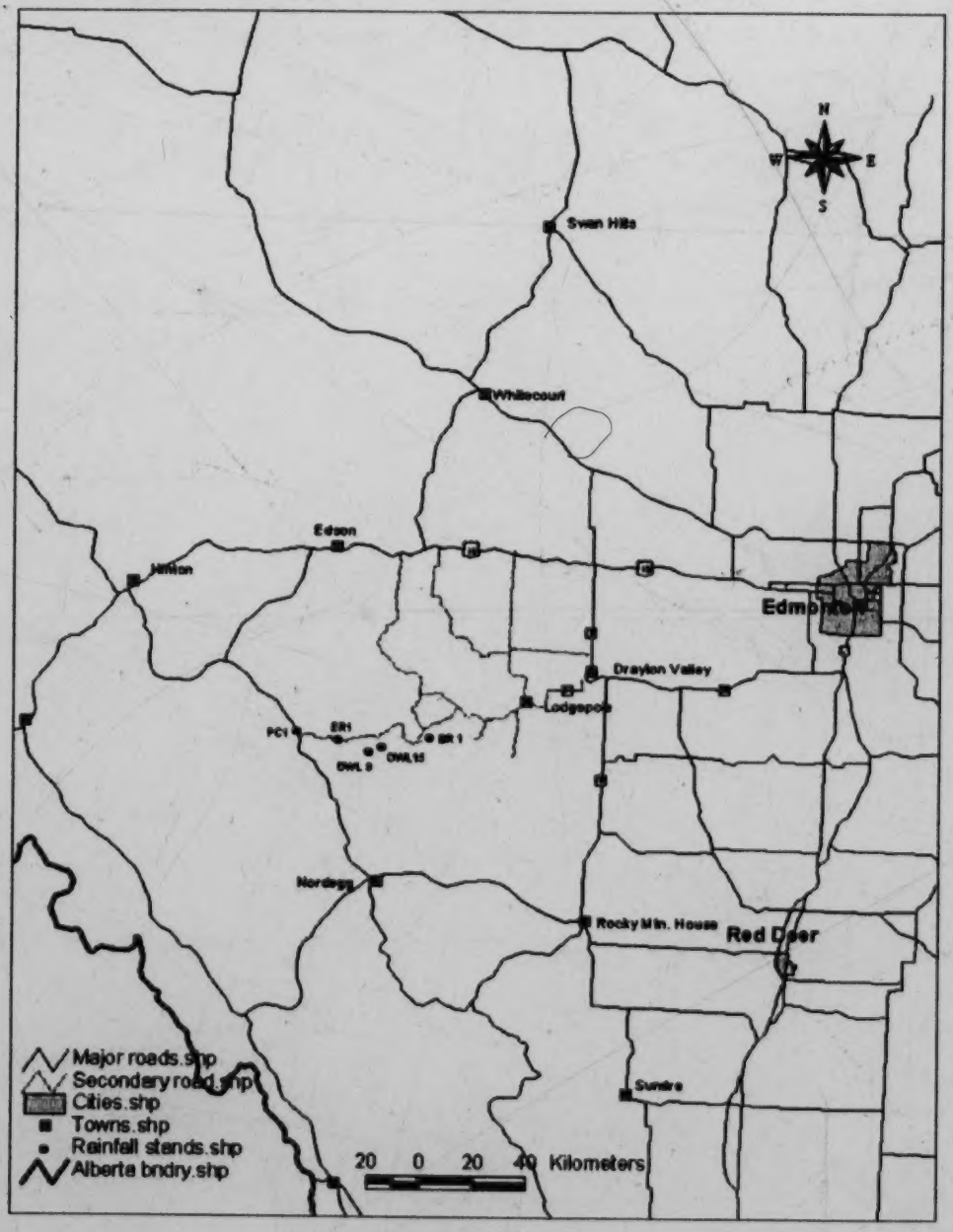


Figure 3-2a) (Top) Photograph showing a throughfall trough and tipping bucket for BR1, b) (Bottom) Photograph showing the distribution of throughfall troughs for ER 1.

Figure 3-3a) (Left) Stemflow collar and collection hose for a tree at PC 1 shortly after a rainfall event, and b) (Right)Photograph showing a stemflow collar and spacers for a PC 1 tree.

Table 3-1 Stand characteristics for all five rainfall interception stands.

Stand Name[a]	Latitude (Deg, Min)	Longitude (Deg, Min)	Subregion[b]	Stand Age	Site Index	Density (tph)	Average Stand Height (m)	Total Volume (m^3/ha)	Basal Area (m^2/ha)	LAIe (m^2/m^2)
OWL-15[d]	52 54.8454	-116 05.779	11	30	22.1	3600	9.2	134.5	24.9	3.2
PC-1[d]	52 56.7918	-116 35.002	10	36	18.0	7000	9.1	199.9	39.4	2.6
BR-1[f]	52 57.5256	-115 50.103	11	61	18.1	2800	15.8	400.6	44.8	3.0
ER-1[f]	52 55.6500	-116 21.120	11	113	18.3	1250	20.6	495.2	44.7	1.8
OWL-9[f]	52 53.7564	-116 10.089	11	115	13.9	3100	17.2	443.2	45.8	2.6

[a] Stand Name: [d] refers to drag scarified stands, and [f] refers to fire-origin stands

[b] Subregion: 10 refers to Upper Foothills Natural Sub-Region, 11 refers to Lower Foothills Natural Sub-Region

Table 3-2 Gross precipitation and throughfall for all five stands for the summer of 2003 and 2004.

Summer 2003				
Stand	# Events	Gross Rainfall (mm) (Pg)	Throughfall (mm) (TF)	TF as % of Pg
Owl 15	36	102.8	67.6	65.8
PC 1	37	104.5	64.6	61.8
BR 1	27	51.7	34.0	65.8
ER 1	51	89.4	56.3	63.0
OWL 9	41	132.0	81.8	62.0
Summer 2004				
Stand	# Events	Gross Rainfall (mm) (Pg)	Throughfall (mm) (TF)	TF as % of Pg
PC 1	21	90.8	67.6	74.4
ER 1	39	169.9	114.2	67.2

Figure 3-4a-e) Rainfall event size distribution for the 5 stands a) OWL 15, b) PC 1, c) BR 1, d) ER 1, and e) OWL 9.

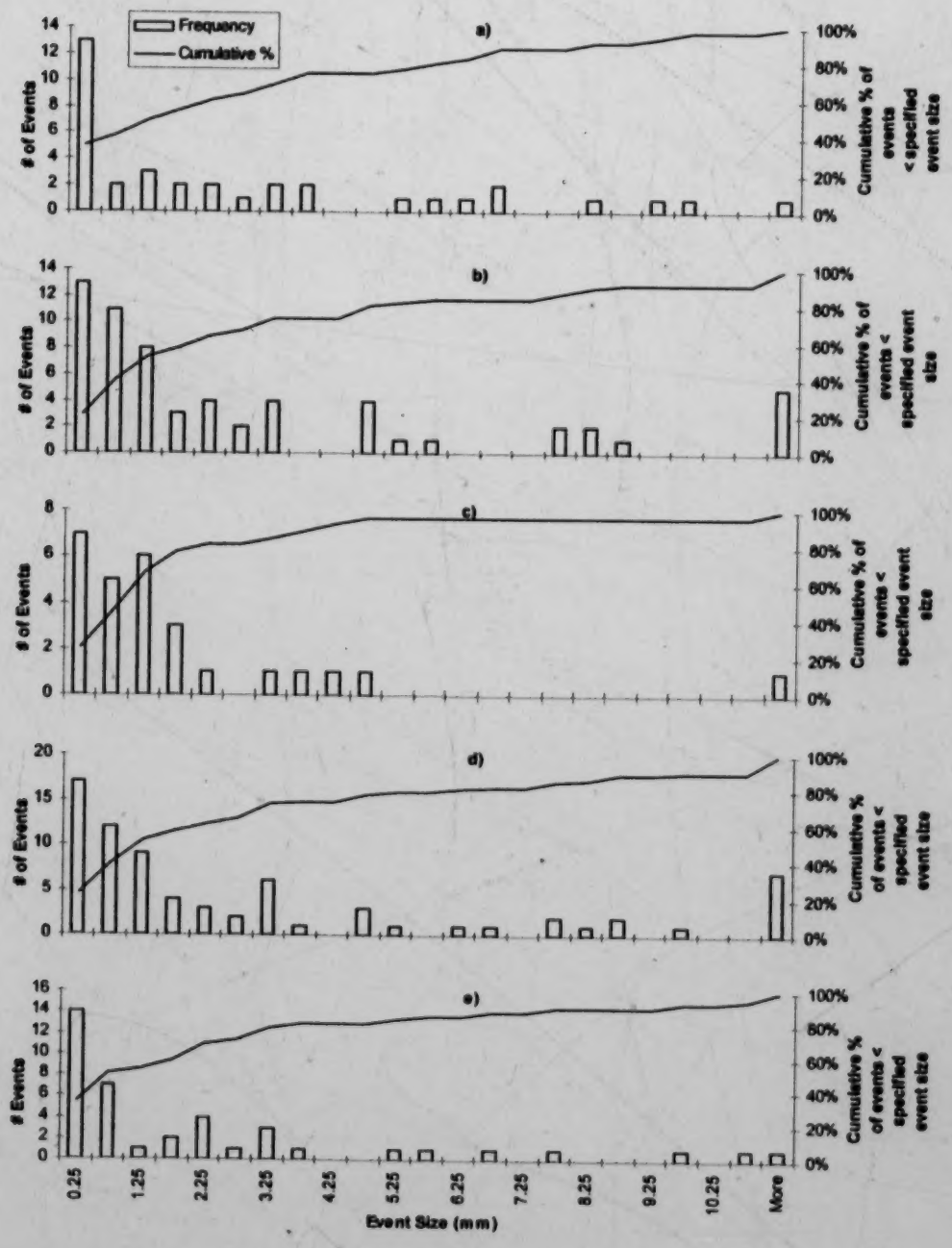
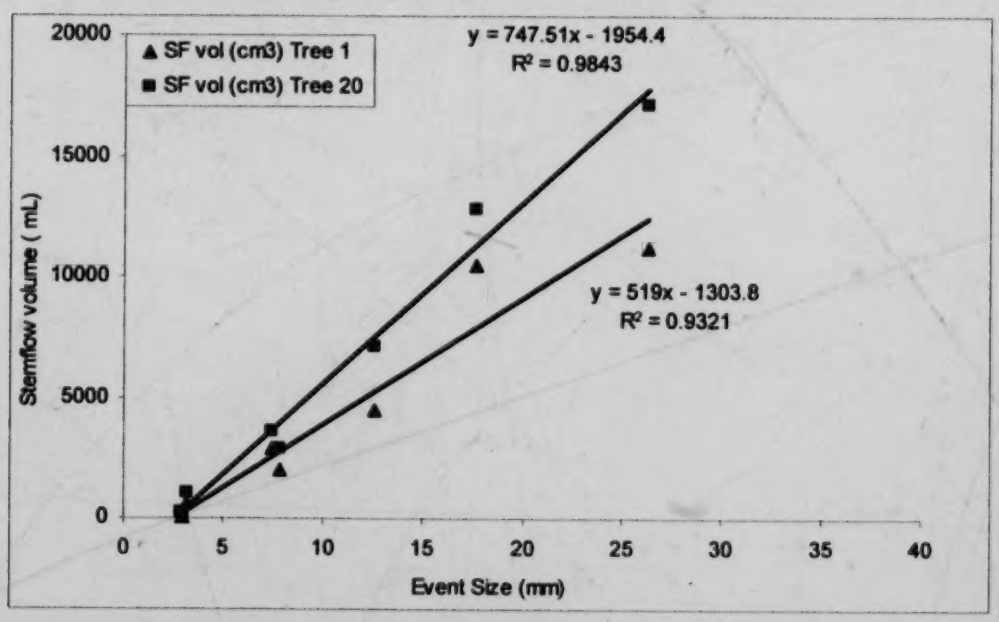


Figure 3-5a) (Top) Stemflow volume/rainfall event size relationship for the PC 1 sample trees, and b) (Bottom) Stemflow volume/rainfall event size relationship for the ER 1 sample trees.



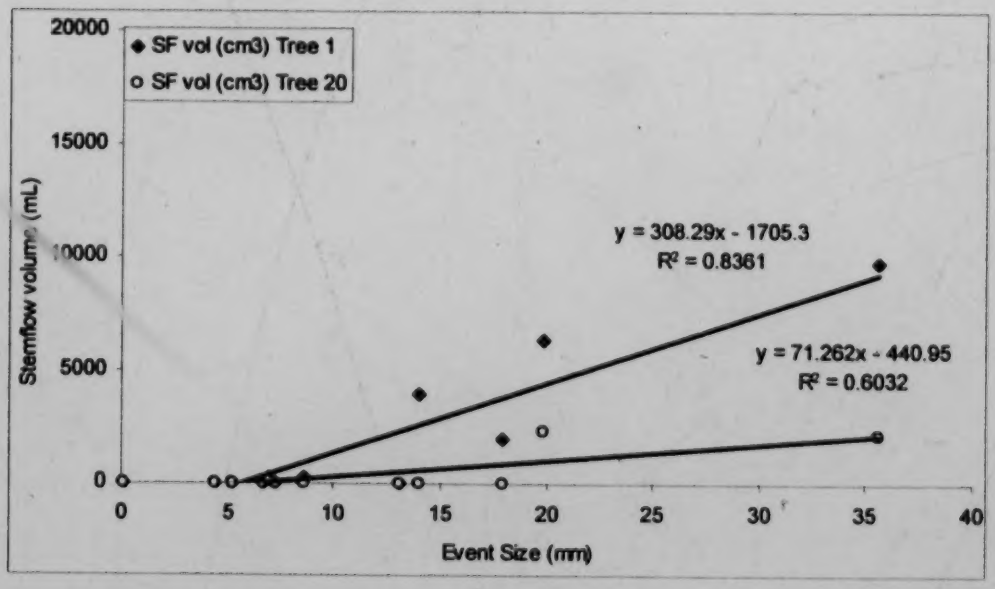


Table 3-3 Stemflow sample tree characteristics for PC 1 and ER 1.

Stand	Tree #	Diameter (cm)	Height (m)	Basal area (cm^2)	Threshold event size (mm)	Bole surface area (BSA) (m^2)	Leaf Area (LA) per tree (m^2)	Tree Volume (m^3)
PC 1	1	11.8	9.0	109.4	2.5	1.7	10.6	0.05
PC 1	20	15.9	9.9	198.6	2.6	2.5	10.4	0.09
ER 1	1	30.9	24.7	749.9	5.5	12.1	35.7	0.83
ER 1	20	20.4	20.8	326.9	6.2	6.7	5.5	0.32

Figure 3-6 Predicted stemflow response for increasing event sizes for all five stands (note: the regression lines for ER1 and OWL 9 are overlapping)

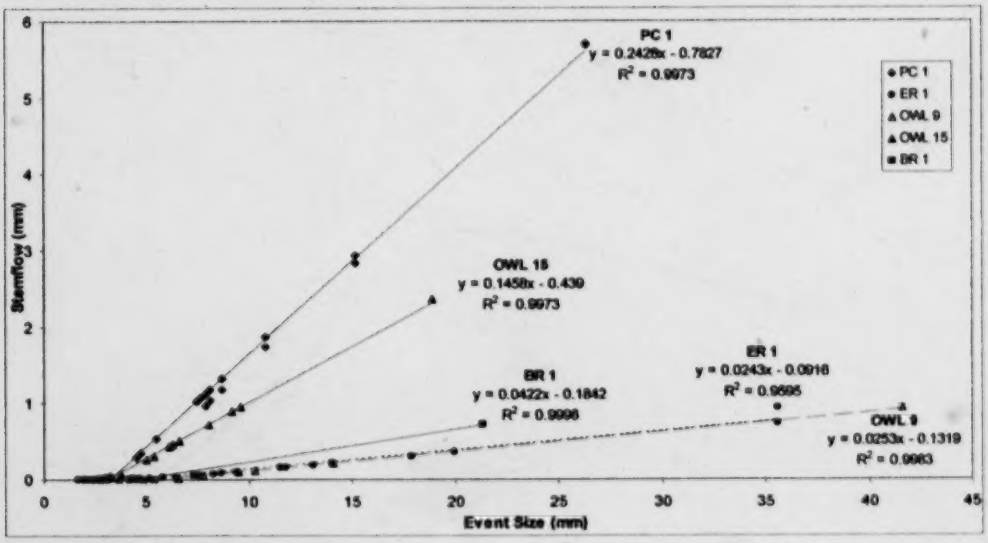


Table 3-4 a) (Top) Summary of predicted stemflow for all five stands, and b) (Bottom) Summary of interception values for all five stands.

Stand	# Events	Threshold event size (mm)	Gross Rainfall (mm) (Pg)	Predicted Stemflow (mm) (SF)	SF as % of Pg
Owl 15 [a]	36	3.0	102.8	7.0	6.8
PC 1 [b]	58	3.2	195.3	18.1	9.3
BR 1 [a]	27	4.4	51.7	3.4	6.6
ER 1 [b]	72	3.8	259.3	2.7	1.0
OWL 9 [a]	41	5.2	132.0	1.4	1.1

[a] refers to stands measured during 2003 only

[b] refers to stands measured during 2003 and 2004

Stand	# Events	Gross Rainfall (mm) (Pg)	Interception (mm) (I)	I as % of Pg	Storage Capacity (mm) (S)[c]
Owl 15 [a]	36	102.8	28.2	27.4	1.1
PC 1 [b]	58	195.3	45.0	23.0	1.7
BR 1 [a]	27	51.7	14.3	27.6	3.2
ER 1 [b]	72	259.3	86.1	33.2	4.0
OWL 9 [a]	41	132.0	48.8	37.0	2.7

[a] refers to stands measured during 2003 only

[b] refers to stands measured during 2003 and 2004

[c] refers to α in equation 3-2

Figure 3-7a-e) Rainfall interception as a percent of gross precipitation for a) OWL 15, b) PC 1, c) BR 1, d) ER 1, and e) OWL 9.

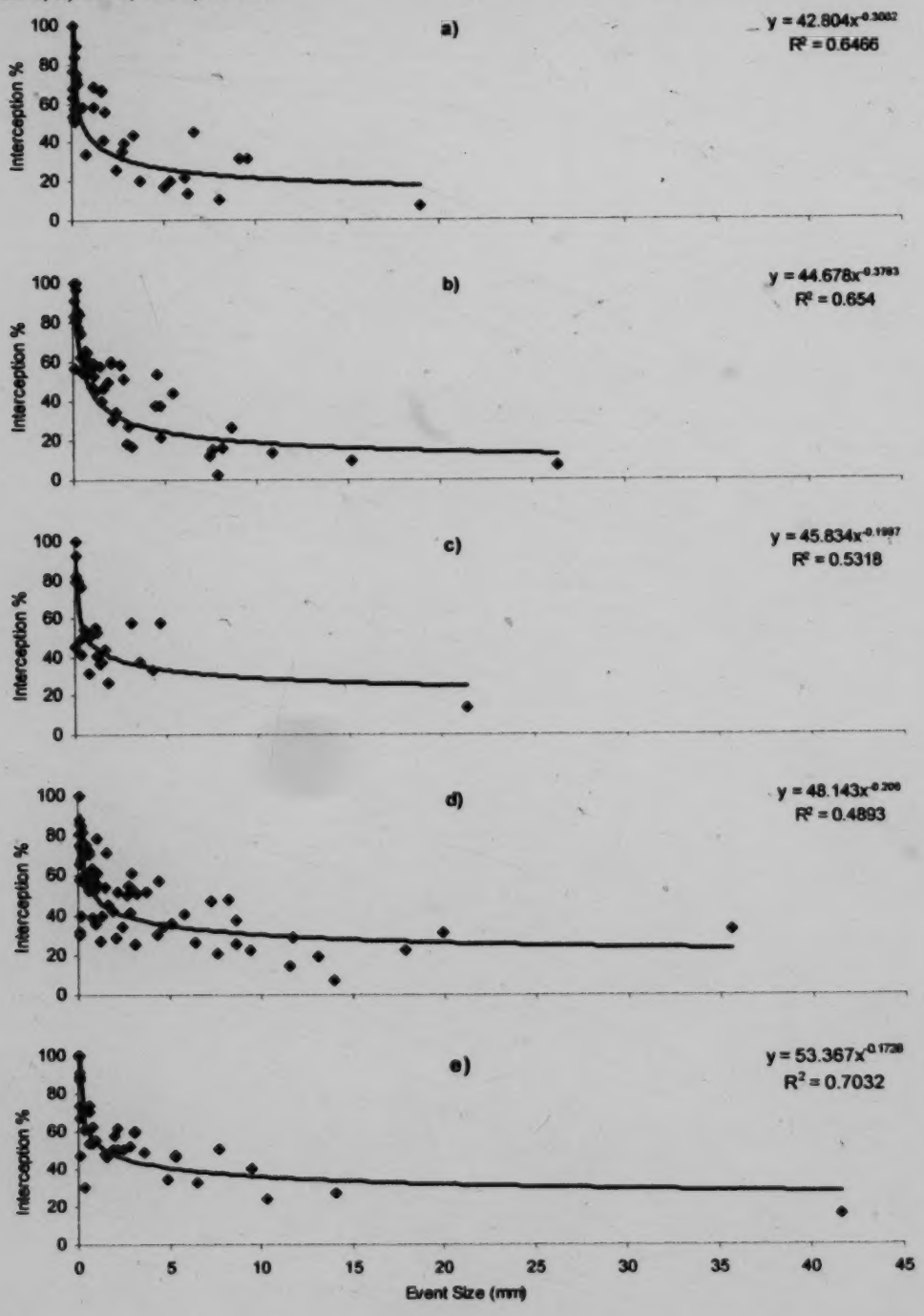


Figure 3-8a-e) The relationship between rainfall interception (mm) and event size (mm) using Equation 3-1 for: a) OWL 15 (α= 1.056962, β= 1.90124, and γ=0.394695, r^2= 0.88, $p<0.0001$). b) PC 1 (α= 1.726284, β= 1.632826, and γ=0.760867, r^2 = 0.84, $p<0.0001$), c) BR 1 (α= 3.232672, β= 3.180113, and γ=0.880175, r^2= 0.99, $p<0.0001$), d) ER 1 (α= 3.960359, β= 3.907754, and γ=0.882231, r^2= 0.91, $p<0.0001$), and e) OWL 9 (α= 2.709305, β= 2731305, and γ=0.75969, r^2= 0.97, $p< 0.0001$).

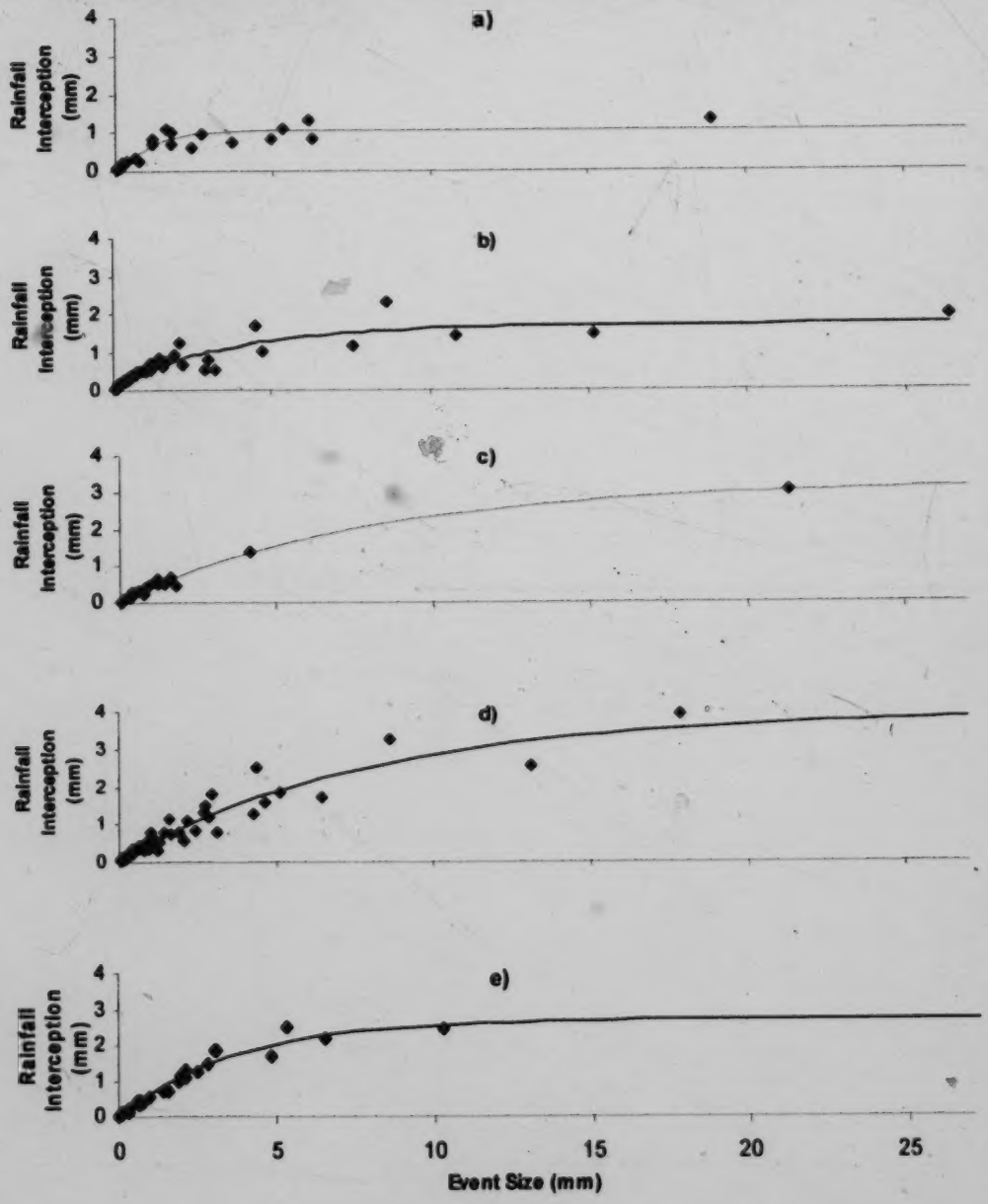
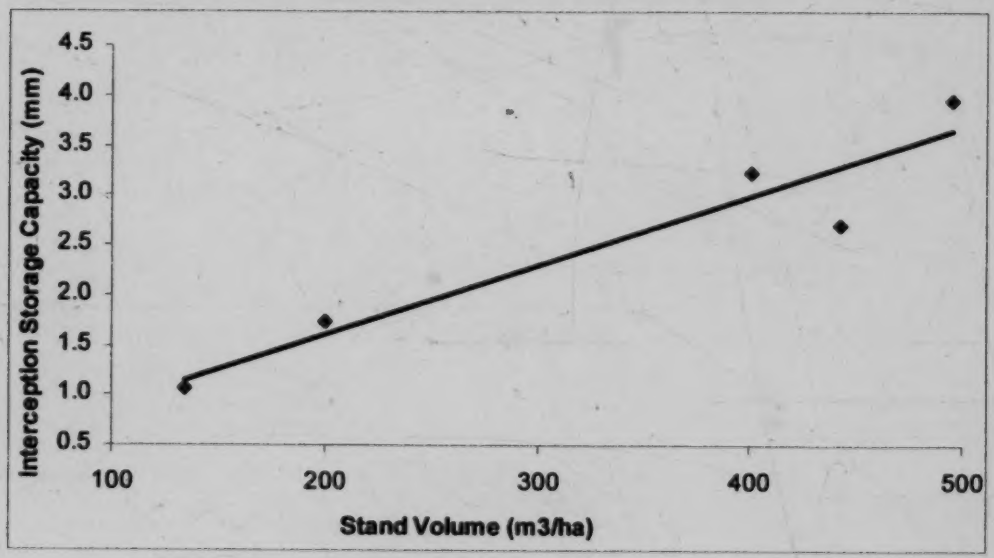


Figure 3-9 Relationship between rainfall interception storage capacity (S) (mm) and total stand volume (m^3/ha) for the five stands. ($y=0.007x + 0.2073$, $r^2=0.9047$, $p=0.01286$).



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Chapter 4 Synthesis

The overall objective of this research was to determine if rainfall interception processes measured at the tree or stand level could be adequately described using easily measured or readily available stand attributes in order to provide the basic tools required to scale interception processes to the landscape level. The first study (Chapter 2) evaluated the relationships between effective leaf area index (LAIe), stand age and volume growth for twenty-nine lodgepole pine stands. The results from Chapter 2 clearly illustrate that canopy leaf area increases rapidly in the early phases of stand development in lodgepole pine reaching a peak between 20 and 30 years. The pattern of development in LAIe with stand age that I observed in this study is consistent with the relationships others have found for lodgepole pine (Long and Smith, 1992) and other early successional species (Gholz, 1986; Kira and Shidei, 1967), however, the rate of change in LAIe, the timing of peak LAIe, and its subsequent decline are dependant on a number of factors including site quality.

Although variation in LA:SA ratios with age has been previously reported for individual trees, the present study is the first (to my knowledge) to show a clear change in stand level LA:SA ratios in maturing stands. Numerous studies (Kaufmann and Troendle, 1981; Kaufmann et al., 1982; Pearson et al., 1984; Dean and Long, 1986) have used leaf area sapwood area ratios (LA:SA) as the basis for allometric approaches to estimate stand or landscape level LAI, however, my results provide additional rationale for questioning the usefulness of this approach to scaling leaf area in forests.

The results from this study showed that LAI predicted from allometric equations (Long and Smith, 1988; Dean and Long, 1986) agreed favorably with measured LAIe, despite differences in climate between Alberta, Wyoming, and Utah. Although Long and Smith (1988) argued that their equation was robust across stands with variable productivity (unbiased with respect to SI), I found that by restricting my analysis to stands constituting a narrower range of SI ("good" sites only) the relationship of measured LAIe to LAI predicted using allometric relationships improved.

The results from Chapter 2 also show that there are both strong linear relationships in LAIe with periodic annual increment (PAI) and very similar trends between LAIe & age and PAI & age. In my study, PAI peaked at 9.9 m^3/ha/year at 25 years coinciding in time with the peak in

LAIe. Although previous research has not been particularly successful in establishing these relationships for multi-aged (Kollenberg and O'Hara, 1999) or even-aged stands of lodgepole pine (Dean et al., 1988; Smith and Long, 1989; Long and Smith, 1990), the generally good relationships I observed were likely due to the fact that I restricted my sampling to stands within the same productivity class.

The relationships I observed between LAIe, PAI, and growth efficiency (GE) with stand age were all generally similar with maximum GE, LAIe and PAI, all occurring at approximately 25 years. Consistent with findings of Long and Smith (1992) for lodgepole pine and Waring (1983) for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), I observed no relationship between GE and LAIe, PAI, or other stand characteristics such as SI or stand density despite strong similarity in the pattern of GE, LAIe, and PAI with stand age. Although there was no direct relationship between density and GE for the stands in this study, the relationships between density and crown length and between crown length and GE were strong. Although density and its influence on live crown depth seem to provide a plausible explanation for the decline in GE, others have suggested that the production: respiration ratio or changes in canopy water relations could be responsible as well (Ryan et al., 2004; Ryan and Yoder, 1997; Mitchell and Goudie, 1980). As it is highly unlikely that one single set of factors govern changes in stand productivity with age, combinations of several factors are probably involved. My results support suggestions by both Smith and Long (1989) that differences in canopy architecture and stand structure in even-aged stands of lodgepole pine directly influence stand volume growth and growth efficiency, and those of Ryan and Yoder (1997) that changes in crown water supply are implicated in declining growth as stands age.

The second study (Chapter 3) characterized rainfall interception processes for five lodgepole pine stands and evaluated the relationships between stand-level interception storage capacities (S) and individual stand attributes. At the outset of this study, it was thought that LAIe would drive interception processes and would therefore explain differences in overall stand interception and S. However, I found that LAIe was inversely related to both interception %, and S, although the relationships were not significant. The results from Chapter 3 suggest that the LAIe of forests is not the only stand attribute responsible for characterizing rainfall interception processes in lodgepole pine forests. Although total stand LAIe ranged from 1.8-3.2, throughfall as a percent of gross precipitation was fairly similar for all stands (62%-74%), and generally increased with increasing LAIe.

The results from Chapter 3 showed that in order to determine an estimate of S, stemflow must be accounted for. The results also showed that the linear regressions between stemflow volume and rainfall event size with individual tree basal area did not provide adequate predictive power to support scaling stemflow relationships to other stands. Therefore stemflow scaling approaches using basal area may be appropriate for scaling within a stand, but scaling the results to other stands may lead to erroneous results. However, the scaling of stemflow volumes from the sample trees to all other trees using total tree height and diameter provided a method of overcoming the problems associated with basal area since these stand attributes probably more closely describe the stemflow generation process. Although several studies have used individual tree basal area (m^2) (Crockford and Richardson, 1990; Herwitz and Levia, 1997) or diameter at breast height (DBH) (1.3m) (Feller, 1981), to convert stemflow volume to an areal basis and to scale stemflow from sample trees to the entire stand (Hanachi and Rapp, 1997), to my knowledge, this is the first time tree height has been used in conjunction with DBH or basal area to scale stemflow between stands. Stemflow values for the stands in this study ranged from 1.0-9.3% of gross summer precipitation and although stemflow values for lodgepole pine are presently lacking in the literature, they are comparable to stemflow studies dealing with other *Pinus* species.

Although stemflow as a percent of gross precipitation was fairly small for the stands in this study, rainfall intercepted by boles can comprise a large component of overall stand interception, since the water-holding capacity of bark is greater than that of foliar surfaces (Herwitz, 1985; Liu, 1998). This has large implications for the stands in this study since most of the rainfall events were smaller than the threshold event size required to generate stemflow. Between 69% and 93% of all events recorded during this study were less than the predicted threshold event sizes for these stands. In other words, all of the predicted stemflow was generated from the very few large events. Therefore, an estimate of stemflow with increasing event size, is required to determine S for these stands.

Rainfall interception as a percentage of gross precipitation ranged from 23%-37% and S ranged from 1.06mm to 3.96mm for the stands in this study. Although, rainfall interception values for lodgepole pine are presently lacking in the literature, these values align themselves with those from other *Pinus* species. Given the relatively small predicted interception storage capacities for the stands in this study, one may think that interception is not very important. However, the amount of rainfall intercepted by these forests plays a large role in determining the

overall stand water balance since most of the rainfall events in this region are less then the predicted storage capacity.

The primary goal of this study was to determine whether rainfall interception processes measured at the tree or stand level can be adequately described using fundamental canopy or stand attributes in order to provide the basic tools required to scale interception processes to the landscape level. Originally it was thought that stand LAIe could act as a scalar to predict S. However, for the stands in this study, LAIe alone could not account for the variability in S. This poor relationship between LAIe and S is likely due to other processes related to stand-level interception storage capacity. Although LAIe is probably a good predictor of canopy interception storage capacity it does not account for the interception storage capacity of boles. However, the average stand bole surface area (BSA) alone couldn't explain differences in S between stands either, but the inclusion of both LAIe and BSA improved the relationship (r^2=0.72, p=0.069).

Actually, overall stand interception storage capacity was better explained using total stand volume. Although this stand attribute directly accounts for the storage component of boles, it may even indirectly account for rainfall intercepted by leaves or needles since the results from Chapter 2 show that stand LAIe is related to the rate stand volume growth. To my knowledge, this is the first time that an independent variable has been identified that was robust with respect to species composition, stand age, and stand condition. Furthermore, total stand volume is an easily measured and readily available stand metric, and a part of typical forest inventories. As a result, the inclusion of total stand volume as an independent variable in processed-based interception models dealing with the characterization of S in forests (at least for these lodgepole pine forests) should be relatively easy and provide reasonable results.

Management Implications

Given the increasing concerns regarding the quantity and quality of Alberta's water resources and the lack of scientific consensus regarding the effect of disturbance on increases in annual streamflow and the magnitude of peakflows, simple models such as ECA-Alberta (Silins, 2000) and WRENSS (Swanson, 2000) have been used by forest managers to estimate the effect of proposed harvesting plans on increases in annual yield. While these models currently use basal area (BA) as the principal stand attribute for predicting recovery of leaf area (hydrologic recovery), my research shows BA is a relatively poor descriptor of LAIe. The use of periodic annual increment (PAI) would substantially improve the predictive capability of both models for

describing changes in LAIe after forest disturbance. Furthermore, the broad availability of forest growth and yield information in most forested regions of North America, and the use of PAI as a predictor of LAIe provide a useful and relatively easy approach to the description of spatial and temporal variability in LAIe across larger landscapes. The characterization of LAIe over broad landscapes will enable the ECA-Alberta model to be used to evaluate relationships between wildfire and streamflow across regional hydrologic gradients from the upper foothills through the boreal plain. A regional hydrologic analysis combined with the results from the ECA-Alberta procedure would enable the prediction of historic and present fire effects on streamflow and will enable an evaluation of each watershed's sensitivity to disturbance in an effort to help prioritize fire suppression efforts.

To my knowledge this is the first rainfall interception study conducted in Alberta dealing with lodgepole pine, and as a consequence, the results from this thesis form the foundation for a more complete understanding of rainfall interception processes in these forests. Although the relationship between LAIe and S was not significant, the results from this study have several implications for the management of forests and water resources. The results from this thesis show that, for lodgepole pine in west-central Alberta, an estimate of total stand volume can be used to predict the stand-level rainfall interception storage capacity (S) of these stands. Therefore, because S is closely related to total stand volume, which is a commonly measured and readily available stand metric, volume could be used to scale S across spatial and temporal scales. This should allow for broader extrapolation of interception results in addition to providing forest managers with insight into how one important component of forest water balance is likely to change as forests establish, mature, and age.

The ability to predict S for forests using a readily available stand metric like total stand volume allows forest managers to control at least one component of the hydrologic cycle when cutting a forest. This has implications for forest managers looking to minimize the magnitude of water table increases following harvesting since the water table rise is caused by a reduction in evapotranspiration, due to decreases in rainfall interception and transpiration (Dubé et al., 1995). The ability to control the magnitude of water table elevation is particularly useful on poorly drained sites where clear-cutting can result in prolonged water table increases which can compromise the establishment, survival, and growth of regeneration (Dubé, et al, 1995; Roy et al., 2000). As a result, forest managers are starting to use shelterwood systems designed to remove a specific percentage of the merchantable basal area (BA) in these problem areas (Pothier

et al., 2003). The results from this thesis have shown that S is more closely related to total stand volume than stand BA. Furthermore, this thesis has shown that larger diameter trees can store more rainfall on their boles than smaller trees (i.e. smaller diameter trees produce more stemflow than larger diameter trees within the same stands). Therefore, the removal of a % of stand volume by diameter class may be a more appropriate method of regulating interception than removing a certain percentage of the stand's basal area.

Future Research

Although this research formed the basis for an understanding of the leaf area-volume growth and rainfall interception dynamics of lodgepole pine in west-central Alberta, it also generated several more questions that need to be answered in order to fully understand and describe these processes over larger spatial and temporal scales. This research was particularly useful in developing tools that would enable the scaling of LAIe and rainfall interception processes to other pure, even-aged lodgepole pine stands (SI>16) in West-Central Alberta, however in order to scale LAIe and rainfall interception processes to the landscape level much work still needs to be done.

1. **Confirmation of leaf area recovery curves for other commercially important tree species across differences in site productivity classes.** Future work should look at the relationships between LAIe, age and volume growth for trembling aspen (*Populus tremuloides* Michx) for "good" and "fair" site productivity classes and for lodgepole pine growing on "fair" sites. If the relationships are robust for these two species, then the general concept should hold for most other tree species as well and will reduce or eliminate the need to define leaf area recovery curves for every tree species. Furthermore, if relationships differ by site quality, existing forest inventory data will enable forest managers to include this variable in the prediction of LAIe. While actual LAI at peak LAIe is probably species specific, once peak LAIe is determined for individual species, the approach of using PAI to describe temporal trends as stands develop and age provides a powerful tool to scale LAIe across space and time.

2. **Designation of canopy and stand-level storage capacity.** Future work should make the distinction between canopy storage capacity and stand-level storage capacity since the latter includes rain stored by foliage elements in the canopy as well as rain stored by boles. Canopy storage implies that either rain or snow is captured by leaves or needles where it

subsequently lost to the environment through evaporation. However, the results from this thesis suggest that tree boles are also an important storage reservoir for intercepted rain. Therefore, in order to determine the total amount of rainfall intercepted by a forest, an estimate of both canopy and bole storage is required.

3. **Determination and characterization of rainfall interception processes for other commercially important tree species.** Future work should look at rainfall interception processes for trembling aspen and white spruce [*Picea glauca* (Moench) A. Voss], as well as mixedwood stands across a range of stand ages and LAIe's. Although S was not related to LAIe for the lodgepole pine studies in this study, relationships between S and LAIe may exist for other species. As these studies have not been previously conducted in Alberta, these results combined with the results from this thesis will characterize the rainfall interception processes for most of Alberta's commercial forests.

4. **Determination and characterization of snowfall interception processes for other boreal tree species.** Because annual precipitation is intercepted as either rain or snow, an estimate of the latter is required to determine average annual interception losses. Although recent physically based models have begun to utilize the relationships between S (for snow) and LAI, for *Pinus banksiana*, and *Picea mariana* in Saskatchewan (Hedstrom and Pomeroy, 1998; Pomeroy and Schmidt, 1993), to my knowledge similar work has not been done in Alberta. Furthermore, to make the results applicable over broad spatial and temporal scales stands of varying ages and LAIe's should be sampled.

5. **Evaluation and characterization of the stemflow generation process.** Because stemflow was only measured on four trees in this study, the inferences based on these results are somewhat limited. As a result, future interception studies should measure stemflow over a wider range of diameter classes and evaluate the prediction of stemflow volume using the height-diameter model developed in this thesis. It would also be interesting to see if these relationships hold for other species, or if other attributes like individual tree leaf area or basal area are better predictors of stemflow volume. Future research should also attempt to characterize the stemflow generation process for other important boreal species like trembling aspen and white spruce. This kind of information is essential to a more complete understanding of rainfall interception processes, because northern boreal forests have been largely under-studied with respect to stemflow generation and nutrient transfer processes (Levia and Frost, 2003). Crockford and Richardson (1990) suggest that the width of the

stemflow collector used affects the amount of stemflow captured. Wider collars will catch more throughfall, and stem/branch drip. Therefore, studies using these larger collectors may actually be over-estimating the amount of stemflow produced by the tree. As a result, this study used plastic collars that shielded the hose, preventing throughfall and stem/trunk drip from being measured as stemflow. It would be interesting to see if stemflow volumes collected by tree differed between trees with and without collars. Although the magnitude of differences is probably species-specific, this information would be invaluable and would likely explain why published stemflow values for specific species vary between studies.

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Appendix 3-1 Tipping Bucket Rain gage Calibration

Individual rain gage calibration was completed in the laboratory at the end of each field season after all of the gages were removed from the field. Rain gage calibration was carried out to determine the average volume (mL) of rain required to produce an event (tip). This was done by filling a 5-gallon carboy with water, measuring its starting weight and slowly delivering water (1-2 drips/sec) via a ¼ inch hose (fitted with a ball valve) to each gage. This procedure was carried out for 30 minutes per gage. Once 30 minutes had elapsed, the flow was stopped and the final weight of the carboy measured. The difference between starting and final weight was determined to be the total volume of water used in the calibration (assuming the density of water is 1 gram/mL). Next, the number of tips, and the average volume per tip were determined. The volume per tip value for each gage was then converted to an area based measurement (area/mm) based on the size of each trough used to collect gross rainfall, and throughfall, in the field